THE UNIVERSITY OF KANSAS

PALEONTOLOGICAL CONTRIBUTIONS

November 30, 1967 **Paper 23**

BRACHIOPOD GENUS ENTELETES IN PENNSYLVANIAN DEPOSITS OF KANSAS

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ABSTRACT

The lowest occurrence of *Enteletes* in Kansas is in upper Missourian rocks of the Pennsylvanian System, where specimens appear in abundance in finely crystalline limestones, generally along the periphery of biostructures in association with the brachiopods *Hystriculina* and *Composita*, corals, and bryozoans. The most diagnostic external characteristics of species of *Enteletes* appear to be 1) distance from the dorsal beak to the origin of the fold and lateral plications, 2) size of the fold angle, and 3) length-thickness ratio as expressed in the reduced major axes, both in slope and intercept. Internally, *Enteletes* is characterized by a prominent median septum, crura-like brachiophore process, and a trilobed cardinal process. Study of shell microstructure reveals the presence of exopunctae and small to large endopunctae. The surface of the shell is ornamented by fine radial costellae, typically 5 to 9 per millimeter in the posterior one-half of the shell.

Previously reported Pennsylvanian species of *Enteletes* which occur in Kansas are here redescribed, discussed, and illustrated with particular emphasis on the nature of the fold. The number of crests on a fold are considered to lack diagnostic significance and accordingly *E. costidorsitriplicatus*, and *E. hemiplicatus plattsburgensis* are judged to be synonyms of *E. pugnoides*. *E. transversus* and *E. hemiplicatus* are regarded as valid species. Three new species, *E. beilensis*, *E. churchensis*, and *E. brownvillensis*, are described and illustrated from the Virgilian, where they occur in moderate abundance.

INTRODUCTION

Previous Studies

The first described species in North America now classed as belonging to *Enteletes* is HALL's (1852, p. 409) *Spirifer hemiplicatus (Enteletes hemiplicatus)*. The specimens studied by HALL are believed to have been collected from the Plattsmouth Limestone along the Missouri River near Weston, Missouri (DUNBAR & CONDRA, 1932, p. 60). HALL's description is very brief and illustrated by a single figure showing what appears to be a laterally compressed specimen.

[1] The project was partially supported by grant 66-67-1 of the Flint Community Junior College Faculty Research Committee.

Subsequent workers (HALL & CLARKE, 1892; BEEDE, 1909) noted variations in the genus, continuing to designate all specimens as *Enteletes hemiplicatus* (HALL).

NEWELL (1931) published the first important paper on Pennsylvanian species of *Enteletes* in Kansas. In this he described three new species, *E. plattsmouthensis*, *E. pugnoides*, *E. transversus*, and a subspecies which he designated as *E. hemiplicatus* var. *plattsburgensis*. His diagnoses are based on general size and shape of the shell, shape of the fold and sulcus, and the ratio between length of the median septum and total length of the shell. Two of NEWELL's species were described on the basis of single specimens. No attempt was made by him to study in detail the internal structures of the shell, the micro-ornamentation, or to determine the stratigraphic range of the species.

In a comprehensive study of mid-continent Pennsylvanian brachiopods, DUNBAR & CONDRA (1932, p. 61) recognized two species, *Enteletes pugnoides*, *E. hemiplicatus*, and the subspecies *E. hemiplicatus* var. *plattsburgensis*. They rejected *E. plattsmouthensis*, considering it to represent merely a gerontic stage of *E. hemiplicatus*, and they questioned the validity of *E. transversus* because it was based on insufficient data and specimens. The collections of DUNBAR & CONDRA extended the range of several of the species.

BRIDWELL (1939, p. 333) briefly discussed the occurrence of *Enteletes* in Kansas and the difficulty in identifying species of the genus. He summarized the work of NEWELL (1931), and DUNBAR & CONDRA (1932), but published one new species named *E. costadorsitriplicatus*. No studies of the genus have been published subsequently.

OCCURRENCE OF ENTELETES

Stratigraphic Distribution

In collecting specimens of *Enteletes*, one is immediately impressed by the apparent consistency of the lithology and the fauna directly associated with *Enteletes*. The geographic distribution is less uniform.

In the Upper Pennsylvanian rocks of Kansas *Enteletes* is abundant in the successive limestones of a specific lithology. Only the "upper" limestones of the megacyclothem (MOORE, 1935, p. 26) contain *Enteletes* in abundance. The genus is less abundant in similar limestone subdivisions of other cyclothems and is rare in most other limestones.

Lowest occurrence of *Enteletes* in Kansas is in Missourian rocks, where it is associated with limestones which may be described as follows:

> Light-bluish-gray to dark-gray, weathering to a light gray or buff; usually wavy to evenly thin bedded, less often even medium bedded; shale partings separating the limestone beds. The limestone is fine-grained, hard, and usually brittle with a moderate amount of argillaceous-arenaceous material present. Sporadic chert nodules and irregular masses of crystalline calcite are characteristic features of the limestone. Thickness ranges from 5 to 15 feet.

Enteletes occurs in Virgilian limestones of the following lithology:

> Light to dark-bluish-gray, weathering to buff or yellowish-brown. The bedding is thin and irregular, generally very wavy, with shale partings separating the various limestone beds. They are fine-grained, hard, and brittle with an appreciable amount of limonite and argillaceous-arenaceous material present. Irregular veinlets of crystalline calcite and local chert nodules characterize the limestone. Thickness ranges from 5 to 15 feet.

In the Captain Creek Limestone (lowermost member of the Stanton Limestone, Lansing Group, Missourian), *Enteletes* occurs in moderate abundance approximately 5 miles north of the Kansas River. Southward, *Enteletes* occurs sporadically but in increasing abundance, reaching its greatest abundance in a "reef" near Fredonia, Kansas. The "reef" is massive and composed of brecciated, fine-grained algal limestone fragments and coarse-grained calcareous matrix with abundant crystalline calcite filling the cavities. Specimens are concentrated in small pockets in the lower talus slope of the buried "reef." *Enteletes* is not found on the upper slopes of the "reef." It is seemingly absent in the Captain Creek equivalent of Oklahoma.

In the Plattsmouth Limestone (upper middle part of Oread Limestone, Shawnee Group, Virgilian), *Enteletes* is found to be widely distributed, varying considerably in abundance but most common in areas surrounding biostromes. DIFFENDAL (1965, p. 112), in discussing a coral bank in the Plattsmouth Limestone in northeast Nebraska, noted the common occurrence of *Enteletes* on the fringe areas of the bank and its absence in other areas. A similar occurrence of *Enteletes* has been noted by me in the Plattsmouth Limestone near Melvern, Kansas. COOLEY (1952, p. 61) noted an abrupt thickening in bedding of the Plattsmouth Limestone in southern Kansas coincident with the presence of superabundant corals and brachiopods, including *Enteletes*. He referred to these occurrences in the Plattsmouth Limestone as biostromes and stated that they are also present northward in the Plattsmouth Limestone.

Brown (1958) made a detailed stratigraphic study of the Beil Limestone, carefully noting its paleontology. He found *Enteletes* in the Beil at only two localities in Kansas. Both occurrences were on the short peripheral slope of a biostrome. Collections made by me from the Beil substantiate the observations of Brown.

Enteletes has been noted to occur in several limestones consisting of marine banks, which suggests a significant relationship between the marine bank and abundance of *Enteletes*. Generally, *Enteletes* is most common on the peripheral slopes and upper edges of biostromes and is rarely found on the upper surface of such structures. Although a complete understanding of marine banks in Pennsylvanian rocks in Kansas is lacking, sufficient evidence suggests an abundant occurrence of *Enteletes* usually associated with the peripheral area of a structure composed essentially of corals and algae.

ASSOCIATED FAUNAS

The fauna found in association with *Enteletes* includes representatives of most of the major marine invertebrate groups of the upper Paleozoic, the associates differing slightly in variety and abundance in each unit in which *Enteletes* occurs. Crinoid columnals, cirrals, and pinnular segments are consistently found. Rugose corals also occur in close association with *Enteletes*; tabulate corals occur in minor numbers. Both ramose and fenestrate bryozoans are usually found; the latter appear to be more consistent in occurrence. Foraminifera, particularly arenaceous forms, constitute an appreciable percentage of the microfauna. Calcareous algae or fusulinids or both occur directly above *Enteletes* in the same lithologic unit, but are only found sporadically in direct association. Although mollusks are found sparingly in most units, they are not directly associated with the genus.

In the brachiopod fauna of a unit where *Enteletes* is present, *Composita* is usually the dominant brachiopod, with *Enteletes* and *Hystriculina* occurring in minor numbers. Where *Enteletes* occurs abundantly, *Hystriculina* is usually moderately abundant and *Composita* less abundant and in many places absent. Other brachiopods (e.g., *Meekella*, *Hustedia*, *Dielasma*, *Neospirifer*) sporadically occur with *Enteletes* within a single unit, but they appear to have no consistent relationship. Of the productids, only *Hystriculina* occurs with *Enteletes*. Where both are present one of them occurs in small numbers. *Enteletes* is rarely found with chonetids.

In marine banks, *Enteletes* is directly associated with essentially the same fauna found with it elsewhere, with a change only in relative abundance. In biostromes the fauna is characterized by the presence of abundant corals, almost forming a coquina. Both rugose and tabulate corals are present; the rugose corals dominate. Algae and bryozoans are present in moderate abundance. The brachiopod fauna appears to be restricted in variety. *Enteletes* is associated with only a few other brachiopods and in some localities is the only brachiopod present. In bioherms, algae are the major element. *Enteletes* is not usually found in direct association with the algae, but is usually found with algal limestone breccia on the talus slope of the bioherm. *Enteletes* commonly is associated with fusulinids.

SHELL MORPHOLOGY OF ENTELETES

The shell of *Enteletes* is characterized by many distinctive morphologic features, several of which are elements of gross shell form.

Lack of adequately preserved shell interiors necessitates placing reliance on external features in discriminating species and for the study of variations within species. Although the mode of preservation obscures detail of the shell interiors, preservation of external features is excellent.

Externally, *Enteletes* is characterized by four major features, shell convexity, fold and sulcus, lateral plications, and fine ornamentation. Less conspicuous but significant features are found in the posterior region of the shell.

CONVEXITY

Enteletes is strongly biconvex, the two valves being nearly equal in convexity, that of the

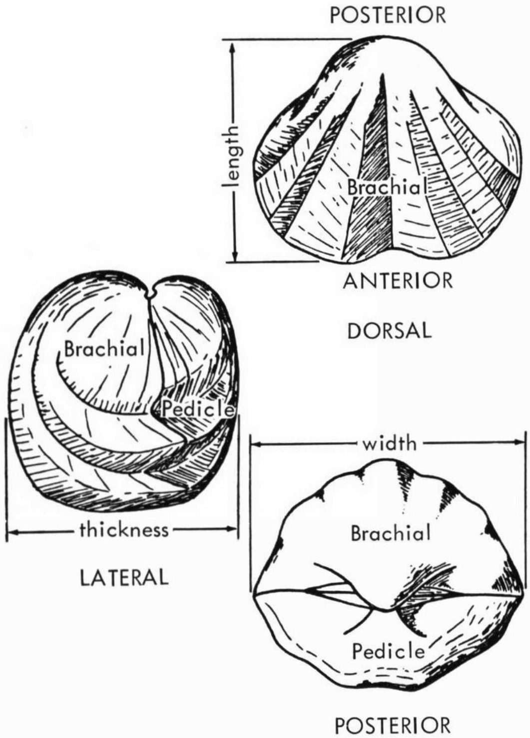


FIG. 1. Standard dimensions and orientation of *Enteletes*.

brachial valve being strongest (Fig. 1). The convexity of the pedicle valve is greatest posteriorly, close to the umbo; the stronger convexity of the brachial valve is approximately at mid-length. These differences are associated with development of the sulcus in the pedicle valve and development of a strong fold in the brachial valve.

During growth of the shell, the vertical component of the growth direction dominates. As the shell grows anteriorly, the vertical growth direction cumulates until a point is reached where the shell ceases to grow anteriorly but only increases in thickness. This point in growth is reflected in the convexity of the valves by an abrupt change in curvature into a low-arched surface nearly perpendicular to the commissure. This low-arched surface is highly imbricated, with greatest development medially, diminishing laterally to the hinge line. The feature is displayed in both valves, but is better developed in the brachial valve, and is referred to as the point of geniculation (Fig. 2). Shell growth after geniculation is characterized by abrupt termination of continuous anterior growth; vertical growth subsequently predominates. The successive lamellae of the secondary shell layer are formed directly on the previous lamella with only slight anterior growth and considerable vertical growth. Internally, the anterior end of the shell becomes thickened.

FOLD AND SULCUS

The most prominent external median feature of *Enteletes* is the very strong, sharply angular fold on the brachial valve, complemented on the pedicle valve by a less pronounced sulcus (Fig. 2).

The fold originates in the anterior portion of the umbonal region of the brachial valve approximately 5 to 10 mm. in front of the beak. The precise distance, within limits, is a very diagnostic feature of individual species. In the initial stages of its development, the fold is very broad, the crest commonly being broad and flat or slightly sulcate for the first several millimeters. During subsequent growth one of two conditions is attained. In most forms, the fold develops a single narrow crest, whereas in others the minor sulcus persists and expands into a permanent feature along the crest of the fold. The significance of this phenomenon is noted in discussion of each species described in this paper. From the initial stage of development the fold becomes progressively more angular anteriorly; the angle subtended by its flanks changes from 179 degrees to a specific range characteristic of the species, generally between 40 and 60 degrees. The fold is most acute at the point of geniculation in stages of late maturity. After geniculation, the species maintains a constant angularity for the remainder of shell growth. The lateral slopes of the fold originate as low rounded flanks, anteriorly becoming flat and long. Similar trends are noted for the sulcus on the pedicle valve.

The fold and sulcus are expressed only as vertical deflections of the commissure and are not expressed in the radial growth of the shell.

PLICATIONS

A very characteristic feature of *Enteletes* is the presence of several well-developed angular plications on the lateral slopes of the shell (Fig. 2). Each successive plication develops anteriorly and laterally from the previous plication and all are present before geniculation. The distance from the brachial-valve beak to the point of origin of

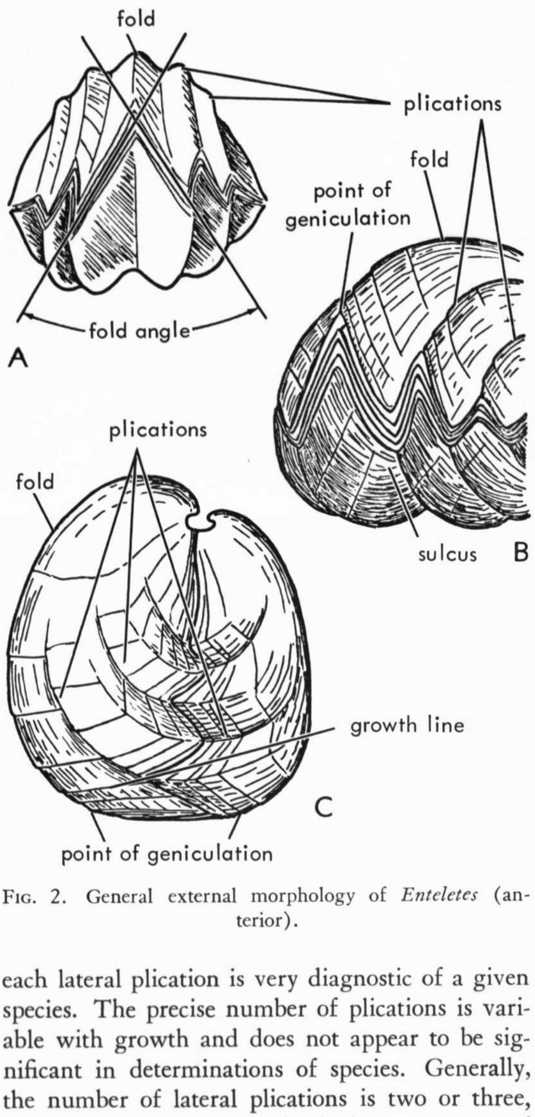


FIG. 2. General external morphology of *Enteletes* (anterior).

each lateral plication is very diagnostic of a given species. The precise number of plications is variable with growth and does not appear to be significant in determinations of species. Generally, the number of lateral plications is two or three, varying on either side of the fold; a maximum of four plications has been observed on a large adult specimen. The plications are very acute, with straight flanks meeting at the apex to form a sharp narrow crest. The angle of the fully developed plications approaches 45 degrees. At the anterior end of the shell the plications form a pronounced angular, zigzag, commissure line. The plications gradually diminish in amplitude laterally, from 5 to 7 mm. in height adjacent to the fold to 0.5 to 1.5 mm. in height along the lateral commissure.

The lateral plications, like the fold, are vertical deflections affecting only the commissure line and not the dorsal outline, and may be referred to as paired serial vertical deflections (RUDWICK, 1959, p. 11).

ORNAMENTATION

Ornamentation is of minor importance as a diagnostic characteristic in *Enteletes*, both at generic and specific levels, particularly the latter. Although ornamentation appears to be an important and persistent element in growth of the shell, other more prominent external characteristics tend to obscure the fine ornamentation of *Enteletes*. The branching system of orthoid ribs was first discussed in detail by BANCROFT (1928) and later elaborated by BANCROFT (1945), and WILLIAMS & WRIGHT (1963). BANCROFT (1928, p. 60) noted that the ribs were added in regular sequence and devised a notation to describe them, a system that he thought was applicable to all orthoid brachiopods. The particular specimens on which BANCROFT based his notational system were moderately coarse-ribbed forms, with ribs which could be readily seen and traced. To expand his notation of a predictable system of rib addition and notation to include all orthoids, both coarse- or fine-ribbed, or both, without actually testing each genus would seem to be presumptuous. The application of BANCROFT's rib notation to *Enteletes* would be very difficult, since fineness of the costellae, their subtle branching, and very early development on the shell make any accurate measurements virtually impossible.

The radial ornamentation of *Enteletes* consists of small, closely spaced, flat-topped costellae. Approximately 10 costellae originate within 0.5 mm. in front of the beak, forming the primary set. The costellae branch and gradually increase anteriorly in width and number. In *Enteletes*, both bifurcate and lateral branching appears to be present. The bifurcations occur usually in the posterior one-half of the shell, forming two costellae of equal size. The lateral branching dominates in the anterior one-half of the shell, forming two costellae of unequal size; the smaller branch obliquely projects anteriorly from the main costellae. The dominance of lateral branching coincides with the development of the lateral plications, where there appears to be a preference for lateral branching to develop down-slope on the fold, sulcus, and plications. The branching of the costellae is very subtle; the paired costellae are in direct contact for an appreciable length before a well-developed

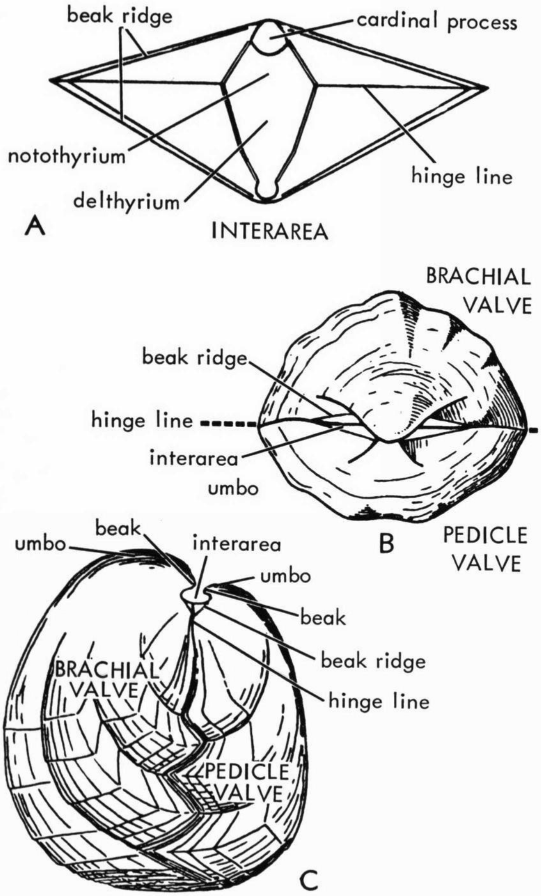


FIG. 3. General external morphology of *Enteletes* (posterior).

interspace appears, particularly with lateral branching. The interspaces between costellae are very narrow, approximately 0.1 of the width of the costellae. Medially, the costellae are very straight; lateral costellae curve outwardly, increasing in curvature posteriorly. The sizes of the costellae vary slightly, both anteriorly and laterally. Anteriorly, the costellae change in width from 0.125 ($\pm$0.005) mm. in width, changing medially up to 0.180 ($\pm$0.005) mm., depending on distance anterior from the umbonal region. The costellae are similar in shape, size, and branching in both the pedicle and brachial valve.

The concentric ornamentation of *Enteletes* consists of growth lines in varying degrees of development. The valves of *Enteletes* are separated into two distinct areas by the line of geniculation, each area characterized by its own concentric ornamentation. From the line of geniculation the valve is usually very smooth, interrupted only by a few irregularly spaced growth lines. These growth lines consist of slight but abrupt changes in the shell surface, formed when radial shell growth temporarily ceased. When radial growth was resumed, it was at a slightly lower plane. The growth lines increase in magnitude and frequency anteriorly, culminating at the line of geniculation, where they maintain the increased magnitude and frequency indefinitely. Along the line of geniculation, shell growth changes direction and rate; the shell no longer grows anteriorly but thickens vertically. The anterior area of the shell after geniculation consists of a series of successive lamellae that occur obliquely to the surface. Each successive lamella extends slightly beyond the previous one, giving the anterior area of *Enteletes* an imbricated appearance.

INTERAREA

The interareas of Pennsylvanian species of *Enteletes* in Kansas are orthocline to apsacline, low, triangular, and curved (Fig. 3).

The pedicle interarea is apsacline and is largest; it is approximately equidimensional, with height slightly less than width and sides slightly concave. Along each side of the interarea, a distinct beak ridge that originates near the beak bounds the interarea down to the hinge line. At the apex of the interarea the sides join to form a low arch. The surface of the interarea is a variably curved plane. Three distinct parts of the interarea are noted, based on the changes in curvature. The change in curvature between the apical part and the middle part is very pronounced, whereas curvature change between the middle and basal parts is less pronounced. The three areas are also characterized by a change in shape of the delthyrium.

The interarea of the brachial valve is orthocline and smaller than that of the pedicle valve. It is low triangular in outline, with weakly concave sides, and has well-developed beak ridges formed at the juncture of the remainder of the valve with the interarea. The sides join to form a broad, low-arched apex. The base of the interarea along the hinge line forms a moderately developed ridge. The surface of the interarea forms two distinct curved surfaces; the first, located in the apical region, is small and flat; the remainder of the interarea is moderately concave.

The surfaces of the interareas are characterized by the presence of well-developed horizontal ridges formed by shell growth. These growth ridges are the result of a sequence of plates with surfaces slightly inclined to the general slope of the interarea. It is this microimbrication structure that forms the prominent ridges. Vertical striae are suggested, caused by the alignment of successive rows of punctae.

DELTHYRIUM

Located in the median portion of the pedicle interarea is a narrow open delthyrium (Fig. 3). The shape of the delthyrium is triangular, with moderately concave sides and height approximately equal to width of the base. The shape may be divided into three segments based on slope of the lateral edges. The initial stage of the delthyrium is characterized by a small circular opening located at the apex of the delthyrium, possibly the result of resorption. Progressive shell growth forms the successive distinct parts, with moderately wide inclined edges. The final part is depicted by more steeply inclined edges and constitutes the largest portion of the delthyrium. Laterally bounding the delthyrium along the edge of the interarea is a faint ridge, gradually increasing in width toward the hinge line. This ridge appears to be the posterior edge of the dental plates. The change in inclination of the delthyrial sides corresponds to changes in the curvature of the interarea and median profile of the specimen. The delthyrium is the opening for protrusion of the pedicle.

NOTOTHYRIUM

Medially located in the brachial interarea is a very small, partially open notothyrium (Fig. 3). The notothyrium is a low triangular opening with moderately convex sides and height less than width. Its apex is partially filled by the cardinal process, restricting the opening to the lower portion. A slight ridge borders the edge of the interarea along sides of the notothyrium. The notothyrium is the brachial complement of the pedicle delthyrium and resembles it in size and shape.

MORPHOLOGY OF INTERIOR

A precise description of internal features of Pennsylvanian species of *Enteletes* in Kansas is difficult to present because the articulated nature of specimens makes any direct three-dimensional observations impossible. The ensuing discussion and descriptions of internal features of *Enteletes* are based on observations of a posterior-to-anterior series of serial sections. The sections were made at right angles to the plane of symmetry of the specimens at intervals of 0.1 to 0.5 mm.

MORPHOLOGY OF BRACHIAL-VALVE INTERIOR

The important and diagnostic internal features of brachial valves are essentially confined to the posteromedian cardinalia. The cardinalia include features associated with articulation, lophophore support, and muscle attachment (Fig. 4).

DENTAL SOCKETS

A pair of small, well-developed dental sockets are present. These appear as conical chambers converging posteromedially on either side of the notothyrium. They are bounded medially by the brachiophore, ventrolaterally by the shell wall, and dorsally by well-developed fulcral plates. The dental sockets function as the receptacle for hinge teeth and act as a fulcrum for articulation. The sockets appear to be relatively uniform in the genus and are not useful for differentiation of species.

BRACHIOPHORES

A pair of thin, laterally divergent blades of secondary shell material project from either side of the notothyrium to form the brachiophores, which consist of two elements: brachiophore base and brachiophore process. The brachiophore base is a thin, anteriorly divergent, triangular-shaped plate that connects the brachiophore process to the interior of the brachial valve. It originates slightly in front of the notothyrium, developing anteriorly 5 to 10 mm., depending on stage of growth. The brachiophore process posteriorly is a narrow triangular thickened plate on the upper edge of the brachiophore base. Anteriorly, the brachiophore process extends beyond the brachiophore base and develops into a think, laterally concave, ventrally curved ribbon, gradually becoming thinner and

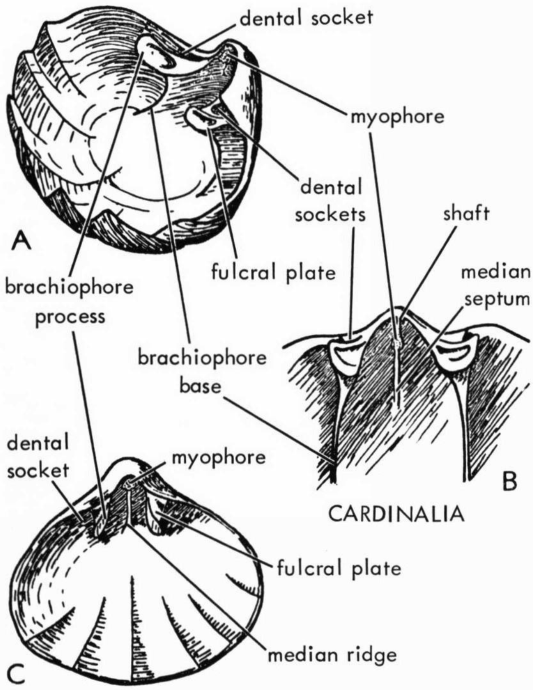


FIG. 4. General internal morphology of the brachial valve of *Enteletes*.

laterally divergent from the mid-line. The brachiophore of *Enteletes* is well developed and may be considered as a crus. The function of the brachiophore process in this genus seemingly is support of the lophophore.

CARDINAL PROCESS

The cardinal process is a weakly developed posteromedian structure consisting of two elements: myophore and shaft. The myophore is a small, trilobed, ventrally pointed, wedge-shaped structure. The primary element is a short bulbous median lobe; the lateral lobes appear to be secondary, consisting of coarse, fibrous material curving outward, giving the myophore a rough texture for attachment of the diductor muscles. The myophore is basally connected to the shaft, which is a thin, weakly developed bladelike structure connecting the myophore to the floor of the brachial valve. In some species it extends anteriorly to join a median ridge.

MEDIAN RIDGE

In the posterior half of several Pennsylvanian species of *Enteletes* in Kansas, a small, low triangular median ridge is developed. The ridge is located anterior to the cardinal process shaft and gradually terminates at mid-length.

MORPHOLOGY OF PEDICLE-VALVE INTERIOR

Two features characterize the pedicle valve interior; the well-developed advancing dental plates and the strong, abruptly terminating median septum. The dental plates divide the posterior part of the pedicle valve into a median delthyrial chamber and two lateral umbonal chambers (Fig. 4). Distinct hinge teeth are also present.

HINGE TEETH

A thickened ridge along the interior edge of the delthyrium culminates into low conical teeth. Anterodorsally teeth rest on the dental plate. The hinge teeth complement the dental sockets of the brachial valve.

DENTAL PLATES

An important and diagnostic feature of *Enteletes* is a pair of moderately oblique, well-developed, advancing dental plates. The thin, triangular dental plates are located beneath each hinge tooth projecting anteriorly from an interedge of the delthyrium to a point of termination at approximately mid-length of the shell. Anteriorly from the hinge teeth, the concave dorsal slope of the dental plates is steeply inclined to the point of termination.

MEDIAN SEPTUM

An equally important and diagnostic feature of the pedicle interior of *Enteletes* is its strong median septum (Fig. 5). This consists of a thin, triangular bladelike structure that originates umbonally and extends anteriorly along the median line bisecting the delthyrial chamber. It gradually increases in height anteriorly, reaching its maximum slightly behind its abrupt termination at mid-length. The crest of the septum is somewhat bulbous.

PUNCTATION

The presence of punctate structures in brachiopods has been known for more than 100 years. CARPENTER (1851) noted and briefly described

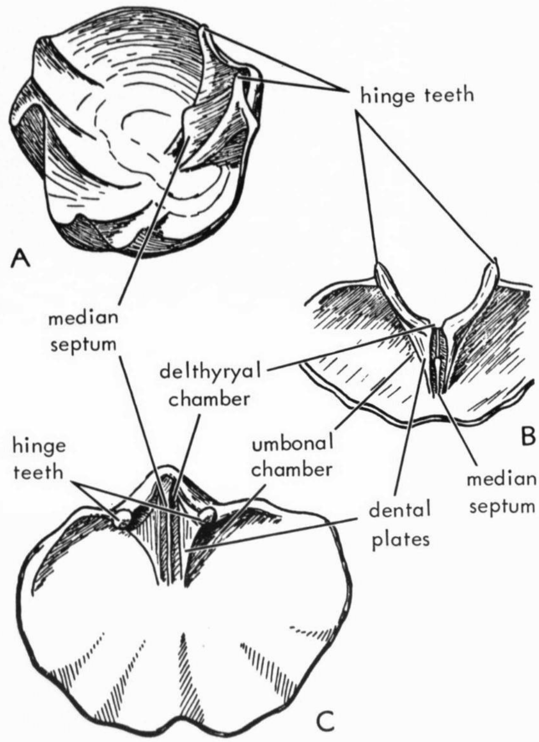


FIG. 5. General internal morphology of the pedicle valve of *Enteletes*.

their occurrence and later (in KING, 1869) he illustrated his observations. Subsequent students (MORSE, 1873, 1902; BEECHER, 1892, THOMSON, 1929) elaborated on CARPENTER's work, and several workers (BLOCKMANN, 1908; BUCKMAN, 1910; PERCIVAL, 1916) attempted to use endopunctate densities to distinguish species, but with varying success. McCOY, for example, was able to differentiate *"Waldheimia" macropora* from *"W." flavescens* based on size and density of punctate, and BLOCKMANN similarly distinguished *Terebratella dorsata* from *T. enzenspergeri*. PERCIVAL, however, was not as successful, for he was unable to differentiate *Terebratula biplicata* from *T. punctata* on the basis of their punctae densities. Recent work by WILLIAMS (1956) on the calcareous brachiopod shell has greatly increased our knowledge of punctation in more modern terms.

The brachiopod suborder Orthidina is subdivided into three superfamilies, partly based on the presence or absence of endopunctae. *Enteletes* is a genus of the punctate superfamily Enteletacea. Although each family and genus may possibly have its own characteristic punctae, certain generalities can be expressed concerning the superfamily. SCHUCHERT & COOPER (1932, p. 24) noted that in the punctate orthoids (enteletaceans) if the shell is costellate, the punctae occur in rows concordant with the costellae. Small punctae are usually found in thick shells and coarser punctae in thinner shells (CLOUD, 1942, p. 24). The endopunctae in *Enteletes* appears to follow these general rules very closely.

LEIHOLD (1925, p. 226) observed two types of punctate structures in the same species of several Devonian orthoids. He noted the variability of pore diameters which tended to form two series, one of large pores, the other of small pores. A careful examination of the endopunctae in *Enteletes* tends to agree with LEIDHOLD's observation.

ENDOPUNCTAE

The absence of the primary layer from the shell of *Enteletes* permits the display of a series of moderately course endopunctae prominently developed along the crest of the costellae. These endopunctae occur initially in a single row. As the costellae increase in width with shell growth, gradually the arrangement of pores is modified to produce diagonal pore pairs (Fig. 6,*D*). Also, the moderately coarse endopunctae are associated with numerous fine, more closely spaced ones located along both edges of the costellae (Fig. 6,*C*).

The fine endopunctae are tubular and uniform in diameter, 0.008 ($\pm$0.005) mm. They are perpendicular to the surface, bending slightly laterally at the base toward the mid-line of the containing costellae.

The course endopunctae in *Enteletes* are tubular in their inner portions and become trumpet-shaped outward. The inner segment is very small in diameter, 0.008 ($\pm$0.005) mm. The outer segment abruptly flares to a diameter of 0.036 ($\pm$0.005) mm. The coarse endopunctae are uniformly perpendicular to the surface (Fig. 6,*C*) and concordant with the costellae, generally equidistant from one another along the crest of the costellae in a single row. In adult shells the coarse endopunctae become more closely spaced anteriorly to the mid-length of the costellae and then are more widely spaced to the margin.

The two types of endopunctae, although different in size and shape, exhibit the same basic rela-

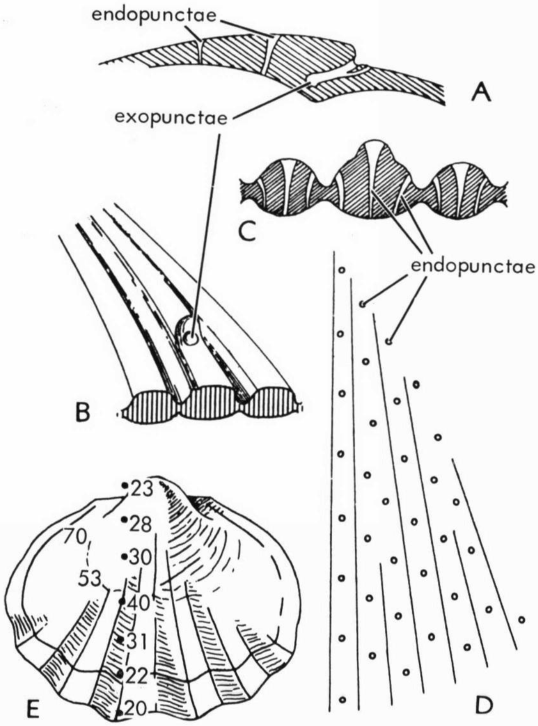


FIG. 6. Features of punctae in *Enteletes*.——*A*. Longitudinal section of shell showing exopunctae (anterior direction toward right), ×10.——*B*. Oblique exterior view of three costellae, middle one with exopuncta at anterior extremity of keel-like structure, ×10.——*C*. Transverse section of three costellae showing endopunctae, ×12.5——*D*. Distribution pattern of endopunctae on fold parallel with growth lines, ×10.——*E*. Endopunctae density (given at 2.8 mm. intervals), ×2.5.

tionship to the costellae. The endopunctae are concordant with the radial ornamentation and occur in a regular arrangement in the individual costellae.

Attempts made by earlier workers to identify species on the basis of density of endopunctae were frustrated by variability of the density in a single specimen. PERCIVAL (1916, p. 52) recognized a definite pattern in the endopunctae density. As the shell grows anteriorly and laterally, the density of endopunctae increases. This pattern is suggested in *Enteletes*, although determination of endopunctae densities in the genus is extremely difficult owing to inability to observe readily all of the fine endopunctae which may be partially obscured by the costellae, by isolated patches of primary shell layers, by rock matrix, or by recrystallization of the shell. Assuming the same percent of error (10%) in recording observations throughout the specimen, the relative endopunctae density within a single shell can be determined with moderate accuracy (Fig. 6,*E*).

Since punctae have been observed, considerable speculation has been published on their possible mode of formation and function. WILLIAMS (1956, p. 246-247) described the formation of endopunctae as follows:

> Each caecum first appears along the inner surface of the lobe as a small bud consisting of a few large cells, but does not "grow out" from the surface of the epithelium until it reaches the tip. At this stage it is cup-shaped and is connected with the periostracum by numerous fine cytoplasmic strands, the brush, radiating from a membranous cover to a conical lumen. As the caecum migrates posteriorly along the tip of the outer lobe, two or three elongate cells charged with a mucin-like substance appears with the lumen. The entire secretory portion of the caecum to the tips of its brush is completely encased in the calcite of the primary layer and its essential cup shape is retained throughout the length of the shell. At the junction of the primary and secondary layers a stalk, connecting the cup with the outer epithelium, is formed in a manner illustrative of the complicated differential growth of the brachiopod shell. The posterior face of the stalk is buttressed by calcite fibers disposed at oblique angles to the primary layer; but along the anterior face there are a number of fibers extending to the outer epithelium which clearly were never contiguous with the primary layer and which were therefore formed by cells originating posterior to the primary-secondary junction. The general growth of the terebratuloid shell and at least all other punctate ones is therefore an expression of three components of growth: first, an expansion directed inwardly and obliquely to the form of the shell consequently to the continuous secretion of shell, a second resulting from the migration of epithelial cells from a primary generative zone at the closed end of the mantle groove, and third, an inward growth, normal to the primary layer, resulting from the activity of a second generative zone at the primary-secondary junction.

The function of the endopunctae is still unknown, although two possibilities have been considered. The first is that in some manner they aid the respiratory or excretory system of the animal to function better by increasing the surface area of the epithelium exposed to the exterior. The second is that they act as protective devices to discourage encrusting organisms from attaching themselves to the exterior of the shell.

EXOPUNCTAE

One of the most diagnostic features of the radial ornamentation of the enteletaceans is a series of gradually raised ribs which abruptly terminate in shallow pits. SCHUCHERT & COOPER

(1932, p. 42) referred to these structures as exopunctae, stating that they are readily visible on the exterior shell surface; and that the exopunctae occur in the primary layer, penetrating only the upper portion of the secondary shell layer, never passing completely through the entire shell.

In the Pennsylvanian species of *Enteletes* in Kansas, exopunctae are observed on the exterior of the shell as small circular pits, 0.1 ($\pm$0.03) mm. in diameter, located at the anterior terminal end of a long prominent keel-like structure superimposed on a normal costella. The length of the keel-like structure ranges from 2.0 to 3.5 mm. and the width ranges from 0.10 to 0.15 mm. It is generally slightly smaller in width than the costella on which it is placed (Fig. 6,*B*). The formation of the keel-like structure appears to be continuous with the formation of costellae with which it is associated.

On the interior surface of the shell, no distinction can be made between the two structures, suggesting that the keel-like structure is a thickening of the costella; both the costella and the keel-like structure are solid.

In thin section, the interior surface of the keel-like structures appears as a thickening in the shell. As the external keel increases in size, the thickening of the shell on the interior increases at approximately the same rate. At the point where the keel-like structure terminates anteriorly, the interior of the shell sags downward and then resumes normal shell thickness. The exopunctae proper appear in this downward sag as uniform tubular structures inclined posteriorly. Many of the exopunctae in the anterior half of the shell have two or three branches (Fig. 6,*A*). They occur at the surface as a cluster of smaller punctae around the main exopunctae. The length of the exopunctae is 0.25 ($\pm$0.03) mm.

The exopunctae are associated with the radial costellae—more specifically with major costellae. The actual occurrence of the exopunctae proper begins approximately 5.5 ($\pm$0.5) mm. in front of the beak. Where exopunctae proper first occur, they are spaced laterally between every sixth costella. Successive exopunctae occur on costellae midway between costellae previously having exopunctae. More than one exopuncta may occur on a single costella. The development of successive keel-like structures begins 0.2 ($\pm$0.1 mm). anteriorly from the previous exopuncta proper.

The termination of the keel-like structure is related to the stage of development of the structure and usually coincides with the presence of a prominent growth line. Should the keel-like structure be in an early stage of development, the structure will completely transgress the growth line. However, if it is in a late stage of development, the structure abruptly terminates, the characteristic pit occurring slightly posterior to the growth line.

The distribution of the exopunctae is similar to that of the endopunctae. They gradually increase in density anteriorly and laterally.

Williams (1956, p. 250) was first to suggest a possible mode of formation of the exopunctae as result of a

> . . . regularly occurring inward sag of the mantle edge away from the sharply angular margins of the principal ribs, with deposition continuing and ultimately sealing off the re-entrant as a short oblique cylindrical hollow.

His concept of exopunctae formation appears to be applicable to Pennsylvanian species of *Enteletes* in Kansas.

SHELL MORPHOLOGY IN RELATION TO ENVIRONMENT

Based on the characteristics of the shell, certain paleoecologic aspects of *Enteletes* can be inferred.

A very distinctive characteristic of adult *Enteletes* is its nearly spherical shape. Sphericity of brachiopods has been of interest to many students who have attempted to draw some conclusions as to environmental significance of shell shape. Lamont (1934, p. 174) stated that brachiopods with large body cavities in relation to size of the shell generally live in areas of high oxygen content, such as is found in areas with arenaceous bottom sediments. Menard & Boucot (1951, p. 145), in experimenting with the hydrodynamic properties of some modern brachiopods, observed:

> As the variation in shape represents an adaptation to differences in current velocity, the more spherical forms must be those which are best adapted to live where currents are faster. The shape may be related to some secondary characteristic of fast currents such as an increased oxygen or food supply—but if the adaptation of shape is necessary in order to counterbalance the velocity of the water, a more spherical shape must be the one which is least affected by moving water. Therefore, the velocity necessary to initiate motion appears to vary directly with the sphericity.

The fold, sulcus, and lateral plications are also conspicuous elements of the shell of *Enteletes* and form a zigzag commissure. Several interpretations can be made from this commissure pattern. Rudwick (1964) discussed the significance and gave measurements of the zigzag commissure in great detail. He elaborated on the hypothesis of Schmidt (1937, p. 27-30) that the degree of the zigzag slits can be controlled more closely than the opening of a straight commissure. Rudwick (1964, p. 135) stated further: ". . . the presence of species with zigzag deflections does not imply any special environmental conditions." Although the zigzag commissure does not imply any special environmental conditions, it does suggest need of the species to be highly selective as to size of materials allowed to pass through the aperture. The shell of *Enteletes* is very thin, as are most enteletacean shells, and in an area of moderately high energy, such a shell could easily be broken. It is conceivable, then, that the plications of *Enteletes* aided in strengthening the shell, in manner similar to the way in which corrugations strengthen a cardboard box. The development of a zigzag commissure, by increasing the length of the commissure, will also greatly increase the amount of material which can be inhaled and exhaled from the organism. It may be, too, that the plications aid in stabilizing the shell in areas of moderate currents.

I conclude that, although the zigzag commissure may function primarily as an inhalent protective device, it may also perform several other important functions.

The fine radial ornamentation of *Enteletes* appears to have some relationship to environment. The relationship between coarseness of the interspaces between costellae of the brachiopod shell to the size of bottom sediments was briefly discussed by Lamont (1934, p. 176). He stated that the size of costellae interspaces must be nearly the same as the bottom sediments in order to permit maximum stability of the shell on the bottom. *Enteletes* possesses very distinct costellae with interspaces approximately 0.025 (1/40) of an inch. This would indicate that *Enteletes* would be most stable in a depositional environment of fine to medium silt. Insoluble residues have been analyzed from the Captain Creek Limestone, Plattsmouth Limestone, and Beil Limestone and at localities where *Enteletes* occurs in abundance, the insoluble residues contain 40 to 80 percent tan silt aggregate; sand-sized material has not been recorded as occurring with *Enteletes*.

The presence of an open delthyrium and a partially open notothyrium in *Enteletes* suggests the presence of a functional pedicle. The function of a pedicle is to attach the brachiopod to the substratum in a permanent position. Therefore, it can be inferred that *Enteletes* required a pedicle to aid in resistance to some force such as a current.

SYSTEMATIC PALEONTOLOGY

Family ENTELETIDAE Schuchert, 1929

Genus ENTELETES Fischer de Waldheim, 1825

Enteletes choristites Fischer de Waldheim, 1825, Notice sur la Choristite, p. 6.

Enteletes lamarcki Fischer de Waldheim, 1830, Oryct. Gouv. Moscou, p. 144, pl. 26, fig. 6, 7.

Description.—Shell moderately small to large, subspherical, dorsibiconvex in longitudinal profile, with subrounded to rounded triangular dorsal outline; maximum width near mid-length, maximum thickness anterior of mid-length, and length slightly less than width; broad, strongly incurved and swollen dorsal beak and moderately incurved and slightly swollen pedicle-valve beak. Straight narrow hinge line, 0.5 to 0.4 of maximum width. Low, triangular, curved apsacline ventral interarea with small, narrow, high triangular, open delthyrium; extremely low, curved, orthocline to apsacline dorsal interarea with narrow, low, triangular notothyrium, partially closed apically by cardinal process; distinct beak ridge bounding both interareas. Fold usually unicrested, commonly bicrested, rarely tricrested, beginning several millimeters anterior of brachial-valve beak; in transverse section, flanks of fold flat, crest of fold angular, varying from 179 degrees in juveniles to approximately 40 degrees in adults; sulcus less distinct than fold; with one to four lateral plications. Finely multicostellate, costellae low, flat-crested, with narrow deep interspaces, and bifid and lateral branching increasing in frequency anteriorly. Long (2 to 4 mm.), narrow, keel-like ridges regularly distributed in costellae, abruptly terminating as small pits (exopunctae), usually several per costella. Shell thin, with fine punctae occurring as three or four rows concordant with costellae.

Pedicle-valve interior with well-developed,

TABLE 1.—*Comparison of Pennsylvanian Species of Enteletes in Kansas.*

	Adult size (mm.)	Adult fold angle (degrees)	Mode distance (mm.) from brachial-valve beak to origin of fold	plications 1st	2nd	3rd
E. pugnoides	small 13 - 16	48 - 52	6 4 - 9	8 5 - 12	9 6 - 13	10 7 - 14
E. transversus	small 13	68 - 72	6	8	9	..
E. hemiplicatus	large 20 - 24	43 - 47	9 7 - 13	11 8 - 15	12 9 - 15	14 11 - 17
E. beilensis	large 20 - 24	58 - 62	10 9 - 13	14 10 - 15	15.5 12 - 17	15.5 15 - 18
E. churchensis	medium 15 - 18	48 - 52	9 8 - 10	9 8 - 11	9 9 - 13	10 8 - 14
E. brownvillensis	moderately large 19 - 20	48 - 52	11 10 - 13	12 10 - 14	13 10 - 16	14 12 - 15

moderately curved, conical hinge teeth supported by well-developed, advancing oblique, dental plates that slightly converge posteriorly and are parallel to slightly divergent anteriorly, terminating near mid-length. Large, deep, delthyrial chamber bisected by thin, vertical, blade-like median septum that gradually increases in height anteriorly, culminating in point and truncated near mid-length.

Brachial-valve interior with moderately small differentiated cardinal process, consisting of distinct trilobed myophore appearing to develop two lobes with growth, and weak thin shaft commonly terminating anteriorly in low median ridge. Strong brachiophores consisting of large, moderately thin, ribbon-like processes that are laterally concave and vertically curved beyond thin, moderately divergent, advancing bases, dorsal edge of bases extending anteriorly to mid-length. Strong median inclined dental sockets bounded dorsally by well-developed fulcral plates.

Discussion.—The genus *Enteletes* is characterized by an inflated elliptical median profile, subrounded to rounded triangular dorsal outline, and a plicate front dominated by a strong angular dorsal fold (Table 1). The interior is characterized by strong, advancing subparallel dental plates and a large anteriorly truncated median septum (Fig. 2, 3). Pennsylvanian species of *Enteletes* in Kansas are almost entirely defined on variations of these features.

NEWELL (1931, p. 263) used relative size, distance from the beak to origin of the fold, relative angularity of the fold, ratio between length of the median septum and shell as distinguishing criteria of the species he investigated. BRIDWELL (1939, p. 333) used similar criteria to describe *Enteletes costidorsitriplicata*, but attached particular significcance to the nature of the fold.

I collected many specimens from each important stratigraphic unit. The length, width, thickness, fold angle, and distance from the brachial beak to origin of the fold and lateral plications were measured for each specimen. From samples of each stratigraphic horizon were calculated the mean, mode, range, and the variance of these characters (Tables 1,2). The distance from the brachial beak to origin of the fold and lateral plications appears to be an important diagnostic characteristic of a species; although the range of distance for similar species may partially overlap, the mean and mode were used to differentiate species (Appendix 1). The size of a species in terms of its length-thickness ratio was plotted (Table 3), as is the fold angle in particular species (Table 1).

Inability to make direct observations of valve interiors eliminates internal features as readily usable diagnostic characteristics. A study of a sequence of serial sections of a single specimen from several species shows appreciable variation in several internal structures. The trilobed process in *Enteletes* appears to be moderately uniform in most species of the genus with exception of *E. hemiplicatus* which appears to have a bilobed cardinal process. In *E. hemiplicatus* the bilobed

TABLE 2.—*Bivariate Statistical Characterization of Reduced Major Axes of Five Species of Enteletes.*
[x=thickness; y=length; measurements in millimeters]

Statistic	*E. pugnoides*	*E. churchensis*	*E. brownvillensis*	*E. hemiplicatus*	*E. beilensis*
N	133	14	7	21	19
$\bar{x}$	10.9	14.6	15.7	21.3	16.1
$\bar{y}$	12.9	16.1	18.6	21.3	20.5
s_x	3.34	4.10	3.10	0.82	3.10
s_y	1.73	1.97	1.84	0.34	1.84
r	0.896	0.836	0.956	0.598	0.676
OR_x	6 - 23	8 - 22	10 - 18	7 - 25	7 - 20
a	0.685	0.483	0.594	0.415	0.682
s_a	0.0387	0.0105	0.0663	0.0726	0.1151
b	5.43	9.04	9.27	12.46	9.54

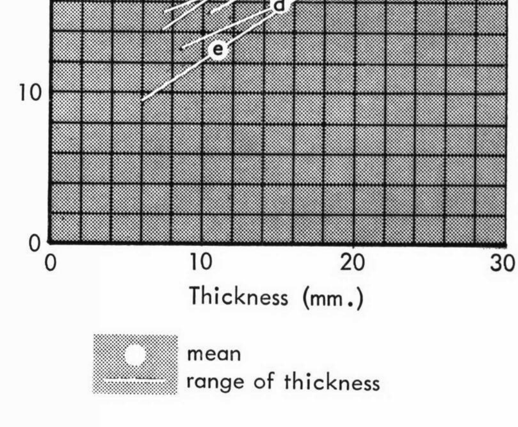
cardinal process may represent a gerontic stage. The brachial median ridge in most species is highly variable. The degree of development of the brachial ridge may be related to growth stages. Insufficient data at this time prohibit comment beyond noting the occurrence of these structures in a single specimen of several species.

Enteletes is a late Paleozoic genus (Middle Pennsylvanian-Upper Permian) of the family Enteletidae (Middle Ordovician-Upper Permian) (SCHUCHERT & COOPER, 1932, p. 119). The ancestral stock of *Enteletes* has been discussed by several workers (WAAGEN, 1884; HALL & CLARKE, 1892; and SCHUCHERT & COOPER, 1932). The first concept of the origin of *Enteletes* was that it came from *Orthotichia* by acquisition of plicae. *Orthotichia* was believed to be transitional between *Schizophoria* and *Enteletes*. However, *Orthotichia* ranges from Pennsylvanian to Permian and is believed to have developed simultaneously with *Enteletes* (SCHUCHERT & COOPER, 1932, p. 147), both being directly derived from *Schizophoria*.

Externally, *Schizophoria* and *Enteletes* are very similar in juvenile stages and become distinct only after the development of a sharp dorsal fold and lateral plications in the latter. Internally, *Enteletes* is distinguished from *Schizophoria* by the presence of strong dental plates and a well-developed median septum. Juvenile forms of *Enteletes* may also be confused with *Rhipidomella* but are distinguished by having a smaller interarea and finer costellae. The adult *Enteletes* is very distinctive and, unless badly damaged, cannot readily be confused with any other Pennsylvanian brachiopod genus. *Parenteletes* is similar to *Enteletes* but differs in the presence of a fold on the pedicle valve. *Parenteletes* has been recorded from only one locality in the Pennsylvanian of Kansas and is generally regarded as a Permian form.

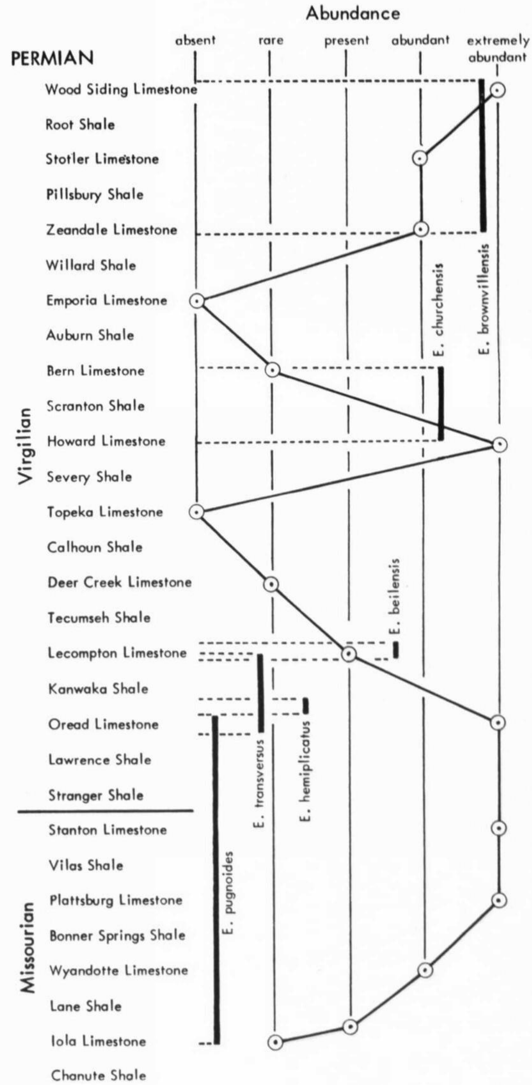
Occurrence.—The geologic range of *Enteletes* in North America is Late Pennsylvanian to Late Permian (SCHUCHERT & COOPER, 1932, p. 146). The lowest occurrence of *Enteletes* in Kansas is in the Iola Limestone (middle Missourian), where it

TABLE 3.—*Reduced Major Axes (Length/Thickness) of Enteletes pugnoides (a), E. hemiplicatus (b), E. beilensis (c), E. churchensis (d), and E. brownvillensis (e).*



occurs locally in limited numbers (Tables 4, 5). In younger Pennsylvanian rocks in Kansas, *Enteletes* is present in nearly every limestone formation, varying in abundance and geographic extent (Table 1). NEWELL (1931, p. 263) made extensive collections in east-central Kansas and found *Enteletes* to occur first "in Miami and Franklin Counties in the Argentine-Farley Limestone, the equivalent of the 'Iola' and Farley Limestone of the Kansas City area." The collections of successive workers (DUNBAR & CONDRA, 1932; BRIDWELL, 1939; and me) verify the lowest occurrence of *Enteletes* reported by NEWELL (1931). I have collected *Enteletes* in several stratigraphic units from which *Enteletes* had not been reported.

TABLE 4.—*Stratigraphic Range and Relative Abundance of Pennsylvanian Species of Enteletes in Kansas.*



ENTELETES PUGNOIDES Newell

Enteletes pugnoides NEWELL, 1931, Jour. Paleontology, v. 5, p. 263-264, pl. 31, fig. 7-11.

Enteletes hemiplicatus var. *plattsburgensis* NEWELL, 1931, Jour. Paleontology, v. 5, p. 265-266, pl. 31, fig. 1-6.

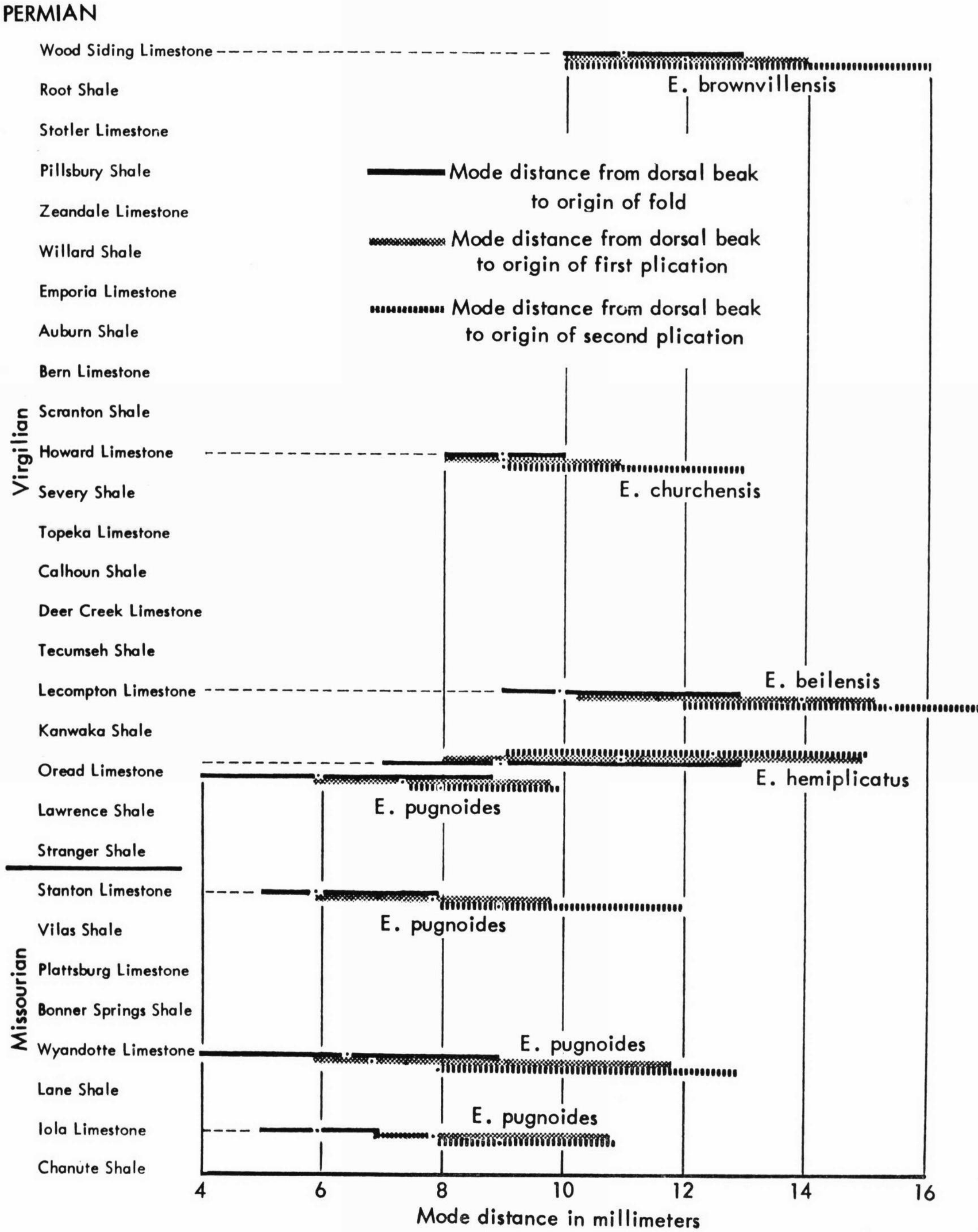
Enteletes costidorsitriplicata BRIDWELL, 1931, Kansas Acad. Sci. Trans., v. 42, p. 330-333, pl. 1, fig. 1-4.

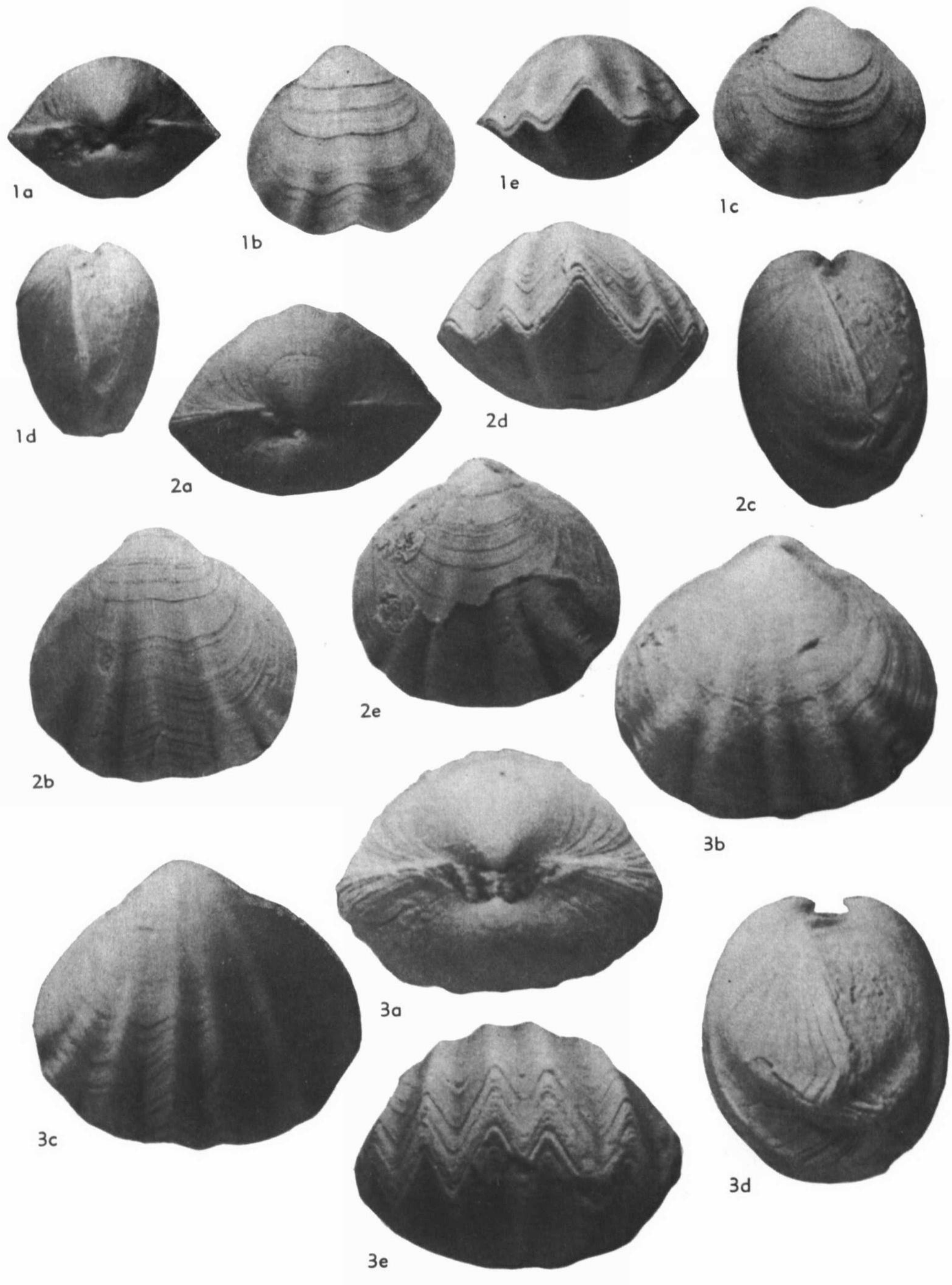
Diagnosis.—Small, subspherical, strongly dorsibiconvex longitudinal profile, broadly rounded triangular dorsal outline; maximum width slightly posterior of mid-length, maximum thickness slightly anterior of mid-length, maximum length less than width; dorsal beak moderately narrow and pointed, strongly incurved; fold usually unicrested, commonly bicrested, rarely tricrested, unicrested fold moderately acute, minimum adult fold angle on anterior surface 48 to 52 degrees, fold originating at moderately short distance from brachial-valve beak, a modal distance of 8 mm. from beak, second plication a mode of 9 mm., and third plication a mode of 10 mm.; radial ornamentation very fine with modal count of 7.5 costellae per mm. at 5 mm. in front of brachial-valve beak, 8 costellae per mm. at 10 mm. in front of this beak.

Discussion.—Under *Enteletes pugnoides* NEWELL, as described by me, are included three previously described species, *E. pugnoides* NEWELL, *E. hemiplicatus plattsburgensis* NEWELL, and *E. costidorsitriplicata* BRIDWELL. The three species were separated on the basis of the nature of the fold; *E. hemiplicatus plattsburgensis*, unicrested, *E. pugnoides*, bicrested, and *E. costidorsitriplicata*, tricrested.

In the adult stage these three forms are readily distinguished, whereas in the juvenile stage they are difficult to differentiate. The juvenile stage of the fold develops as a low broad vertical deflection, a moderately wide and flat crest. The fold must be well developed in the juvenile form or it cannot be determined whether it is unicrested or multicrested. This distinction can usually be made at a distance of less than 1 mm. from appearance of the first lateral plication when the shell is about 7 mm. long. During progressive shell growth in the unicrested form the broad crest becomes nar-

TABLE 5.—*Mode Distance from Dorsal (Brachial-Valve) Beak to Origin of Fold, First Lateral Plication and Second Lateral Plication in Pennsylvanian Species of Enteletes in Kansas.*

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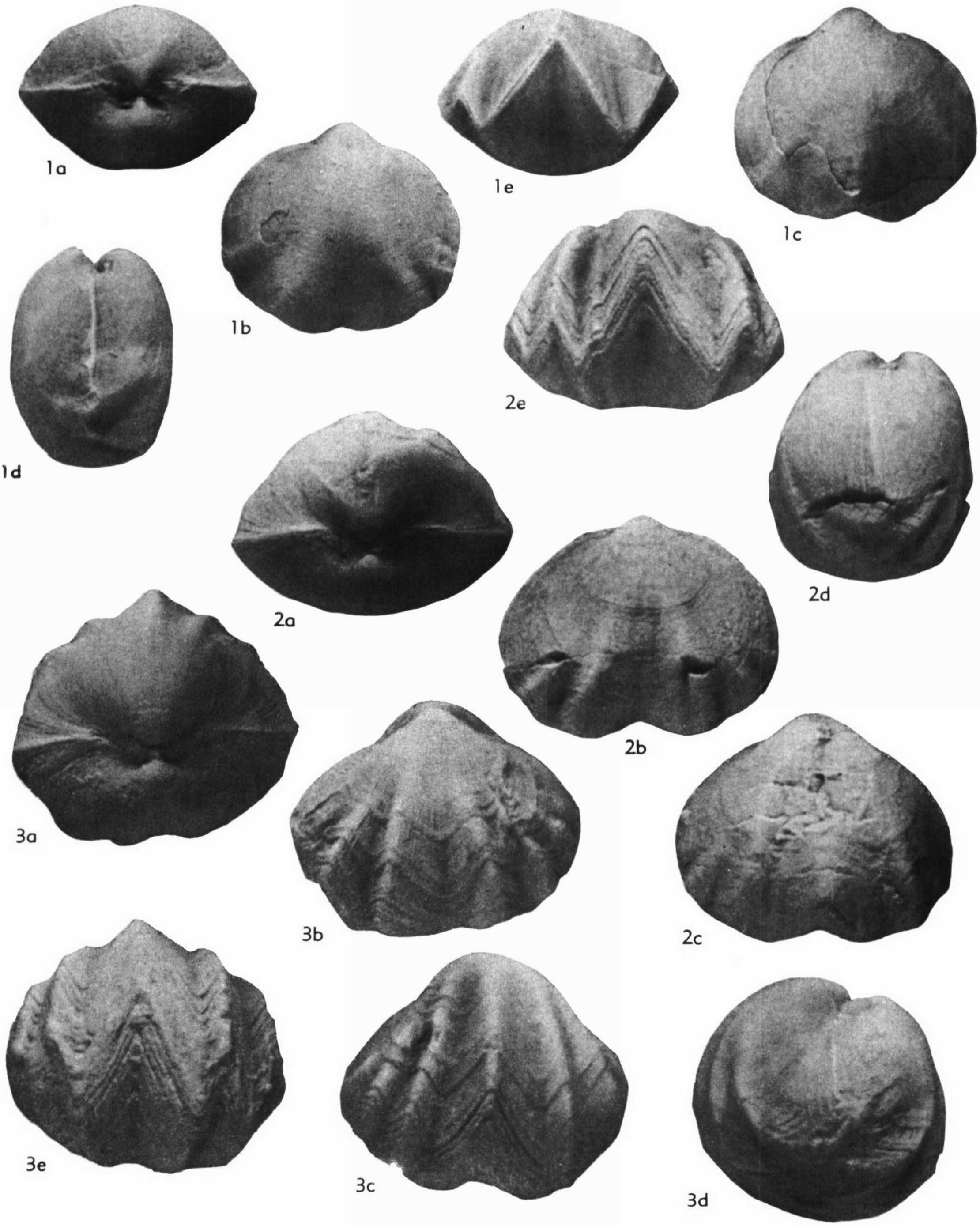
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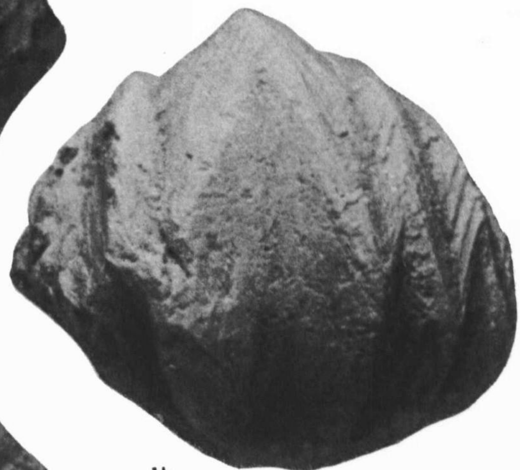

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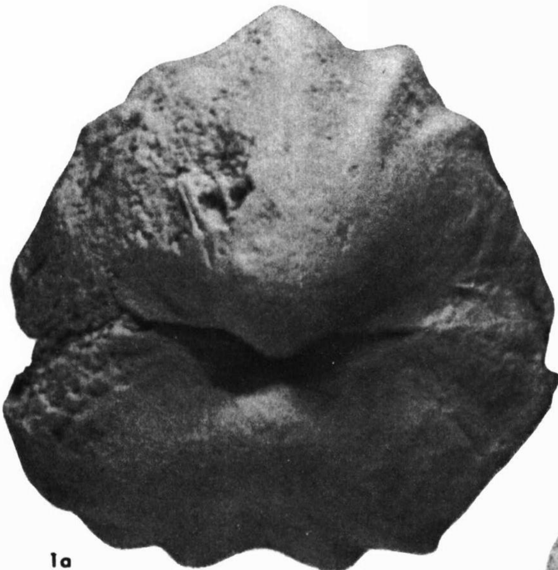

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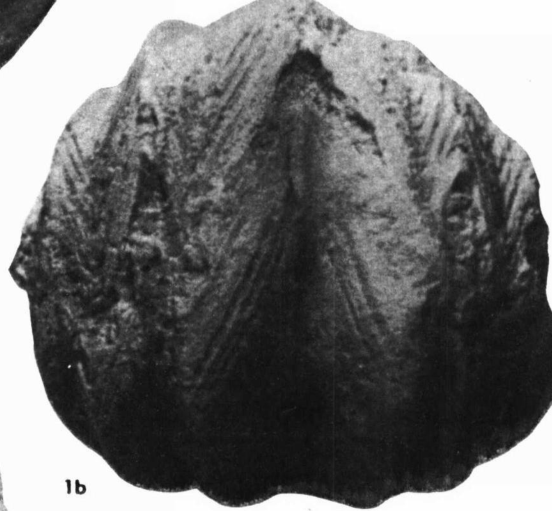

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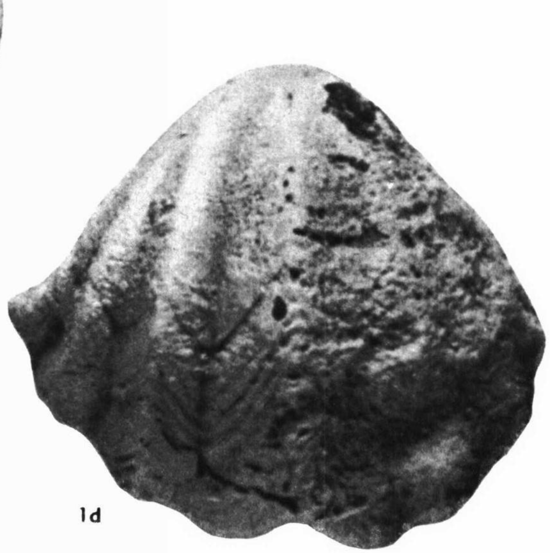

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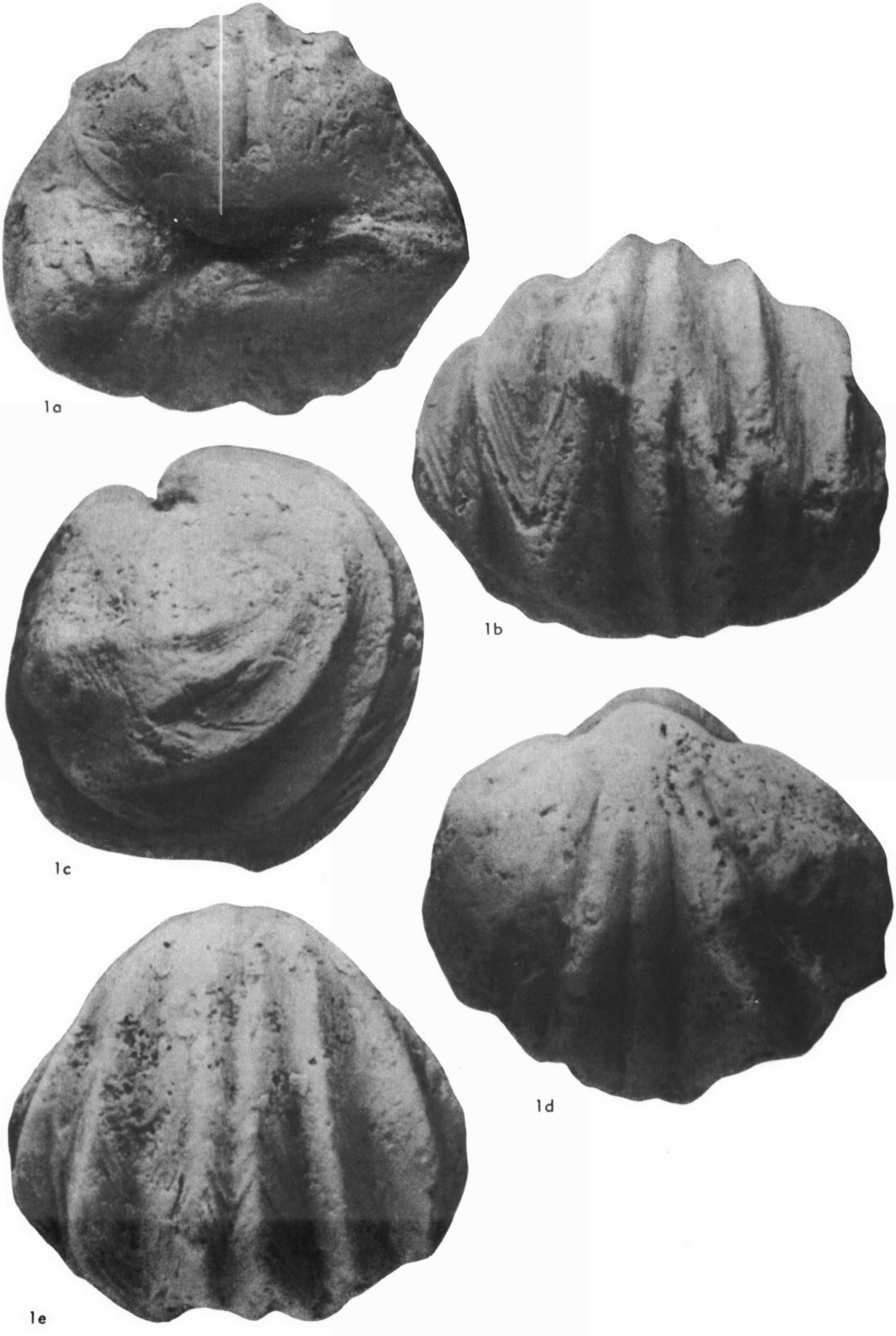
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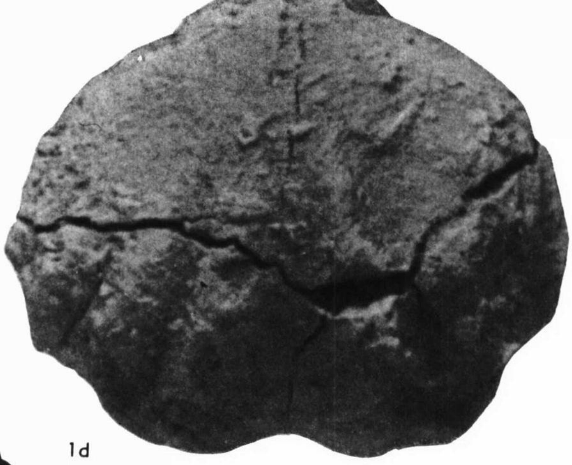

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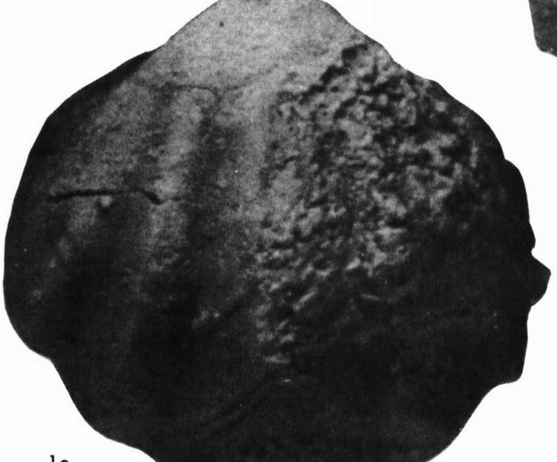

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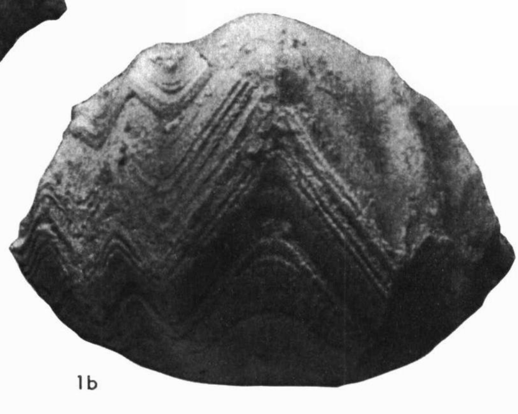

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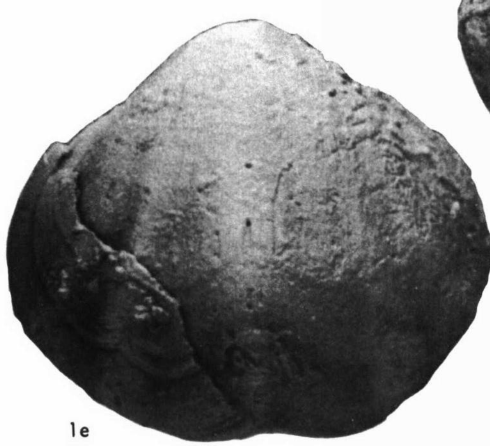

1e

row, anteriorly forming a narrow sharp crest, whereas in the multicrested form the broad fold is maintained with the incipient sulcus developing medially. The occurrence of the incipient sulcus gives rise to two plications on the fold. The degree of development of these two plications is variable. NEWELL (1931, p. 263) described the fold of *Enteletes pugnoides* as being bifid, suggesting that the fold is divided in two by an incipient sulcus. DUNBAR & CONDRA (1932, p. 64) considered the two plications of the fold to be separate in origin. I agree with DUNBAR & CONDRA, although it is very difficult to detect variations in points of origin of the plications in the umbonal region because of the subtleness of the early deflections. A single deflection develops first and is then followed by one or more others; the incipient sulcus does not appear to develop simultaneously with the fold. In later growth stages, many specimens show an appreciable difference in degree of development of the two plications; one may appear lower on the flank of the fold than the other. NEWELL (1931, p. 263) noted that he rarely found transitional forms of folds between the unicrested and multicrested ones. DUNBAR & CONDRA (1932, p. 69) also noted their occurrence but found them uncommon. I admit their rare occurrence, but suggest that this is to be expected. The preconceived notion of the significance of the multicrested fold would cause a worker not to recognize transitional forms, particularly with a feature that requires only a notation of presence or absence. The fact that both NEWELL (1931, p. 263) and DUNBAR & CONDRA (1932, p. 64) admit the presence of transitional folds, regardless of their abundance, is noteworthy.

In a discussion of shell growth, RUDWICK (1962, p. 11) considered two types of vertical deflections, median and paired. The median vertical deflection is in the form of a fold and sulcus; the paired vertical deflections are in the form of lateral plications. The two may occur separately or together. In instances where the two types are combined, they may or may not be ontogenetically related. In *Enteletes*, they appear together, but the median deflection arises independently and earlier than the members of the paired deflection. In juvenile *E. pugnoides* one or more members of the paired deflections may occur sufficiently close to the beginning of the median deflection to be affected by the greater vertical deflection. The median deflection appears to affect a moderately broad area, offering sufficient space for several paired deflections to be superimposed. This moderately broad area rapidly becomes more narrow, prohibiting superposition on the crest. A later paired deflection forms asymmetrical multicrested folds with the paired deflection occurring at various positions down the flanks of the median one. It is significant that forms having multicrested folds usually have an unequal number of lateral plications on the two sides. This suggests that one of the fold plications belongs to the side with the lesser number of lateral plications.

Earlier workers noted the occurrence of a multicrested form but did not agree about its taxonomic assignment. SCHELLWIEN (1900, p. 12) considered it to be a varient of *Enteletes hemiplicatus*, not a separate species; NEWELL (1931, p. 263) judged it significantly different and designated a new species *E. pugnoides*. BRIDWELL (1939, p. 332) collected and described a tricrested form as a new species, *E. costidorsitriplicata*. DUNBAR & CONDRA (1932, p. 65) seemed dubious about the validity of *E. pugnoides* but accepted it on the basis that it was morphologically distinct and appeared to be restricted to a limited stratigraphic horizon.

In my opinion the number of crests in a fold have little systematic importance. The presence of a continuous sequence between unicrested and bicrested folds suggests possible randomness of their development. The number of crests present is solely dependent on the time the strong median vertical deflection occurs in relation to the development of the paired vertical deflections.

With exception of the nature of the fold, all other aspects of the specimens—distance from beak to origin of the fold and lateral plications (Fig. 7); costellae per mm.; length-thickness ratio (Table 3); and absolute size are similar and indicate no basis for differentiation of species. A single set of serial sections (Fig. 8) of several forms indicates that they are similar internally. The trilobed nature of the cardinal process, the size and shape of the median septum, the presence and degree of development of a low median ridge on the interior of the brachial valve, and the thin laterally concave brachiophores are all very similar.

Measurements.—Data on measurements of *Enteletes pugnoides* are given as follows.

Dimensions

figured specimens	length mm.	thickness mm.	width mm.	fold angle
14000	14.0	15.0	17.6	58°
14001	10.0	8.5	11.0	81°
14002	13.0	9.6	14.0	79°
14003	14.6	12.6	16.4	....
14004	13.7	13.2	17.5	63°

Costellae Density (C/mm.)

distance anterior from beak	mode	range	N
5 mm.	7.5	6.5 - 8.5	16
10 mm.	8.0	6.0 - 9.0	12

Distance from Beak to Origin of Fold and Lateral Plications

	$\bar{x}$	s^2	mode	range	N
fold	6.4	1.0	6.0	4 - 9	143
1st plication	7.6	1.8	8.0	5 - 12	266
2nd plication	8.6	1.4	9.0	6 - 13	194
3rd plication	9.8	0.6	10.0	7 - 14	100

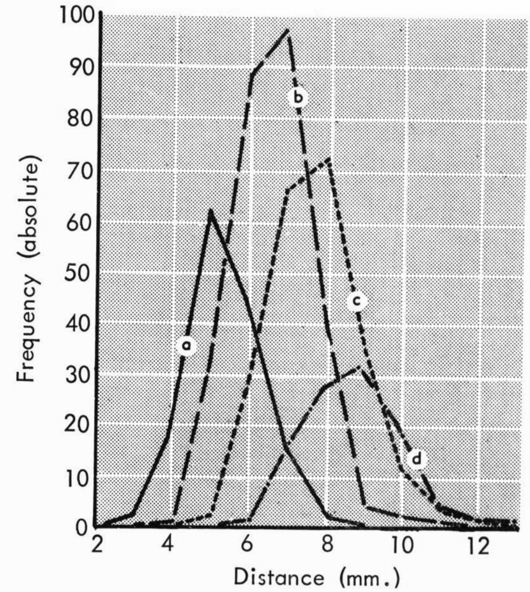

Fig. 7. Graph showing frequency of distances in *Enteletes pugnoides* from brachial-valve beak to (a) origin of fold, (b) first plication, (c) second plication, and (4) third plication.

Occurrence.—*Enteletes pugnoides* is common in late Missourian and early Virgilian rocks of Kansas. The lowest occurrence is in the Iola Limestone and the species is found in most younger limestone members: Argentine-Farley, Spring Hill, Captain Creek, Stoner, South Bend, Toronto, but not above the Plattsmouth Limestone. Throughout the upper Missourian rocks in Kansas, both the unicrested and multicrested forms (bicrested and tricrested) of *E. pugnoides* occur together. In the lower stratigraphic units, the multicrested form is rare, gradually increasing in number upward. Multicrested forms culminate in the Captain Creek Limestone Member (upper Missourian). Virgilian specimens of *E. pugnoides* have been collected only from the Plattsmouth Limestone Member, Oread Formation, where it occurs very abundantly. It is significant that the multicrested form does not occur in the Plattsmouth Limestone.

Illustrations.—Plate 1, figures 1-3; Plate 2, figures 2-3.——Pl. 1, fig. 1a-e, ext. views of specimen (KU 14000) from Captain Creek Limestone, post., dorsal, lat., ant., ventral, all ×2.4.——Pl. 1, fig. 2a-e, ext. views of immature specimen (KU 14001) from Plattsmouth Limestone, post., dorsal, ventral, lat., ant., all ×2.4.——Pl. 1, fig. 3a-e, ext. views of bicrested specimen (KU 14002) from Captain Creek Limestone, post., ventral, dorsal, lat., ant., all ×2.4.——Pl. 2, fig. 1a-e, ext. views of gerontic specimen (KU 14004) from Plattsmouth Limestone, post., ventral, dorsal, lat., ant., all ×2.4.——Pl. 2, fig. 2a-e, ext. views of unicrested specimen (KU 14003) from Argentine Limestone, post., ventral, dorsal, lat., ant., all ×2.4.

ENTELETES TRANSVERSUS Newell

Enteletes transversus Newell, 1931, Jour. Paleontology, v. 5, p. 265-266, pl. 31, fig. 16-19.

Enteletes hemiplicatus Hall (*sensu* Dunbar & Condra), 1932, Nebraska Geol. Survey, Bull. 5, 2nd ser., p. 60-63, pl. 2, fig. 5-8.

Diagnosis.—Small, ovoid, with moderately dorsibiconvex longitudinal profile, broadly rounded, dorsal outline slightly triangular, maximum width approximately at mid-length, maximum thickness slightly anterior of mid-length, maximum length less than width; brachial-valve beak narrow and pointed, strongly incurved; sharply crested unicrested fold, very broad fold angle, 68 to 72 degrees, very wide fold flanks, fold originating at short distance from brachial-valve beak, approximately 6 mm.; lateral plications beginning at mod-

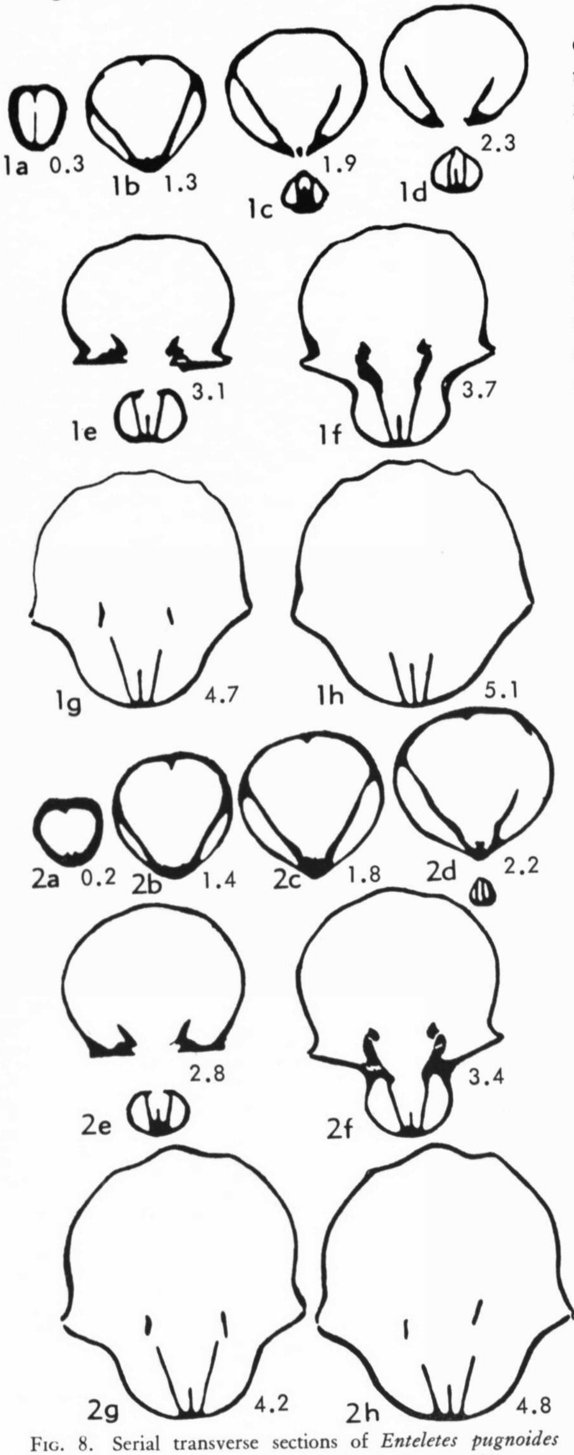

FIG. 8. Serial transverse sections of *Enteletes pugnoides* showing distances from pedicle-valve beak in millimeters. ——*1a-h*. Specimen from Captain Creek Limestone in Leavenworth County, Kansas (sec. 7, T. 12 S., R. 21 E.), ×2.25.——*2a-h*. Specimen from same rock unit and locality, ×2.25.

erately long distance in front of fold, first plication approximately 8 mm. from beak; very fine radial ornamentation.

Discussion.—NEWELL (1931) described *Enteletes transversus* from a single specimen collected from the Lecompton Limestone. The species was distinguished by NEWELL on the basis of a shallow pedicle valve and a broad rounded dorsal fold. DUNBAR & CONDRA (1932, p. 62) were unable to collect a specimen of *E. transversus* and did not consider the single specimen collected by NEWELL sufficient to merit the designation of a new species.

Only a single specimen of *Enteletes transversus* was collected by me; the type specimen is apparently lost and not available for study. The specimen here described is nearly complete, with some of the shell material absent from the posterior part of the brachial valve. The size and degree of development of the fold, lateral plications, and the lack of prominent growth lines suggest that the specimen represents an early mature growth stage. This is seemingly confirmed by the lack of imbricated shell material at the anterior margin, a feature characteristic of old-age growth stages in other species. The fold is approximately twice as wide as the maximum width of any other specimen of *Enteletes* observed. The flanks of the fold extend nearly the full thickness of the specimen. The juncture of flanks of the fold is extremely sharp, considerably different from the usual rounded crest of most species of *Enteletes*. Generally, *E. transversus* closely resembles *E. pugnoides*. The size and proportions are similar, as is the general outline and lateral profile. The distance of the origin of the fold is within the range of *E. pugnoides*. The fold angle is also similar to comparable-sized specimens of *E. pugnoides*.

Enteletes transversus differs strongly from *E. pugnoides* by the wide flanks of the fold.

It may be argued that *Enteletes transversus* simply represents a variation of *E. pugnoides*, that the single specimen collected is an abnormal individual. Variations in the degree of development of flanks of the fold for specimens of similar size would be expected as result of different rates of growth, but specimens of similar growth stages would be expected to show the same degree of development of these features. The width of the fold flanks and the fold angle at the growth stage of the specimen of *E. transversus* is considered to be sufficient to exclude it from *E. pugnoides*.

Measurements.—Information on measurements of *Enteletes transversus* follows.

DIMENSIONS

figured specimen	length mm.	thickness mm.	width mm.	fold angle
14005	13.0	10.5	15.0	72°

DISTANCE FROM BRACHIAL-VALVE BEAK TO ORIGIN OF FOLD AND LATERAL PLICATIONS

fold	6.0 mm.
1st plication	8.0 mm.
2nd plication	9.0 mm.

Occurrence.—The lack of a sufficient number of specimens makes impossible an accurate determination of the stratigraphic and geographic occurrence of *Enteletes transversus.* The single specimen collected by me was found in association with abundant *E. pugnoides* in the Plattsmouth Limestone at a quarry 1 mile north of Melvern, Kansas. The specimen described by NEWELL was obtained from the lower Lecompton Limestone in southeastern Jefferson County, Kansas.

Illustrations.—Plate 2, figure 1a-e, ext. views of specimen (KU 14005) from Plattsmouth Limestone, post., ventral, dorsal, lat., ant., all ×2.4.

ENTELETES HEMIPLICATUS (Hall)

Spirifer hemiplicatus HALL, 1852, Stansbury's Exped. to Great Salt Lake, p. 409, pl. 4, fig. 3a,b.

Enteletes hemiplicata HALL & CLARKE, 1892, Paleont. N. Y., v. 8, pt. 1, pl. 7a, fig. 44, 46-52.

Enteletes plattsmouthensis NEWELL, 1931, Jour. Paleontology, v. 5, p. 262, pl. 31, fig. 20-27.

Enteletes hemiplicatus (HALL), NEWELL, 1931, Jour. Paleontology, v. 5, p. 265, pl. 31, fig. 12-15.——DUNBAR & CONDRA, 1932, Nebraska Geol. Survey, Bull. 5, 2nd ser., p. 60-62, pl. 2, fig. 7, 12, pl. 44, fig. 3-4a.

Diagnosis.—Large, subspherical, with strongly dorsibiconvex longitudinal profile, broadly rounded, dorsal outline slightly triangular, maximum width slightly anterior of mid-length, maximum thickness slightly anterior of mid-length, maximum thickness greater than width; dorsal beak moderately broad and pointed, strongly incurved; with sharply pointed unicrested fold, rare bicrested fold, and very small incipient sulcus; sharply acute fold angle, 43 to 47 degrees, fold originating at short distance from dorsal beak, a mode of 9 mm.; lateral plications beginning a moderately short distance anterior of the fold, first plication a mode of 11 mm. from beak, second plication a mode of 12.5 mm., and third plications a mode of 14 mm. from beak; very fine radial ornamentation.

Discussion.—*Enteletes hemiplicatus* was the first species of the genus to be described from Pennsylvanian rocks of the mid-continent region. HALL figured the type specimen in two views, anterior and lateral. The precise dimensions of the specimen were not given, nor was the scale of the figures. The shell imbrication at the anterior margin of the figured specimen was weakly developed possibly indicating that the shell had attained a stage of maturity.

In redescribing *Enteletes hemiplicatus,* NEWELL collected several specimens from the Plattsmouth Limestone that appear to be similar to HALL's figured specimen. In 1931, NEWELL divided *Enteletes* of the Pennsylvanian of Kansas into three new species and one variety (subspecies), retaining *E. hemiplicatus* as a fourth species. The specimens studied by NEWELL have the characteristics of medium size (length, 16 to 17 mm.; width, 18 to 19 mm.; thickness, 13 to 14 mm.), short hinge line, and ratio of median septum to shell length of 1:2.3. NEWELL further noted that *E. hemiplicatus* can be distinguished easily by the greater angularity and prominence of its fold and sulcus. The specimen figured by him (NEWELL, 1931, p. 263, pl. 3, fig. 7-11) lacks prominent growth lines and the anterior margin of the shell lacks any shell imbrication.

In addition to *Enteletes hemiplicatus* (HALL) as identified by NEWELL, this author also collected large specimens of *Enteletes* from the Plattsmouth Limestone which he designated as *E. hemiplicatus* var. *plattsmouthensis.* This subspecies is very similar to NEWELL's *E. hemiplicatus (s.s.),* differing primarily in size, angularity of the fold, and presence of a well-imbricated anterior margin. His specimens have the characteristics of large size (length, 26 mm.; width, 29 mm.; thickness, 25 mm.), fold originating 10 to 12 mm. from the brachial-valve beak, and ratio of length of median septum to length of shell 1:2.2. The specimens of *E. hemiplicatus plattsmouthensis* figured by NEWELL are very thick, with a highly imbricated anterior margin, and undoubtedly they represent a gerontic growth stage.

DUNBAR & CONDRA (1932, p. 61) collected specimens of *Enteletes* from the Plattsmouth Limestone at the same general locality as HALL's specimens. Their collections consist of a sample of variably sized specimens from points along the Missouri River near Weston, Missouri. The size range of the sample appears to include *E. hemiplicatus plattsmouthensis* NEWELL and *E. hemiplicatus* (Hall) NEWELL which DUNBAR & CONDRA (1932, p. 61) considered to be a late immature form of *E. hemiplicatus.* They interpreted NEWELL's "variety" *plattsmouthensis* to represent a gerontic growth stage of *E. hemiplicatus.*

I have examined the specimens of *Enteletes hemiplicatus* (HALL) figured by NEWELL and concur with DUNBAR & CONDRA that they represent an immature growth stage of *E. hemiplicatus* var. *plattsmouthensis* NEWELL. This conclusion is based on the lack of prominent growth lines and the absence of an imbricated anterior margin. The distances from the brachial valve beak to the origin of the fold are nearly identical for both *E. hemiplicatus* (HALL) by NEWELL and *E. hemiplicatus* var. *plattsmouthensis* NEWELL.

Enteletes hemiplicatus as understood by me, is typified by several characteristics. Adult specimens are moderately large for the genus, but the general proportions of the species are comparable with those of smaller species. Adult specimens approaching 25 mm. in length and 27 mm. in thickness are common, with several gerontic specimens nearly 29 mm. in thickness; the adult width is approximately 29 mm. Geniculation begins at a length of approximately 24 mm.; there the thickness commonly increases at the same rate as early growth stages, whereas both length and width increase at abruptly reduced rates. This growth pattern causes the shape of the shell to become increasingly inflated medially and less spherical. The surface of *E. hemiplicatus* is characterized by the presence of a sharp, prominent, well-developed fold and two to three sharp, lateral plications giving the surface the appearance of being strongly ribbed. The distance from the brachial-valve beak to the origin of the fold distinguishes *E. hemiplicatus* from other species of the genus (Fig. 9), particularly specimens of *E. pugnoides* that also occur in the Plattsmouth Limestone. Although the range of the distance for *E. hemiplicatus* and *E. pugnoides* overlap, the mode of the two species differs by 3 mm. (Table 1). The fold is usually unicrested, with the flanks of the fold approximately twice that of the flanks

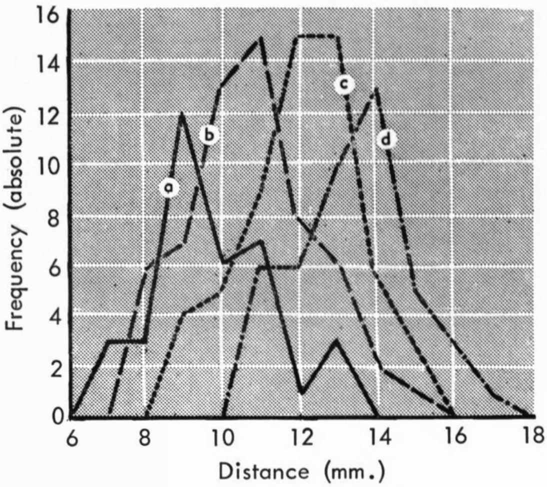

FIG. 9. Graph showing frequency of distances in *Enteletes hemiplicatus* from brachial-valve beak to (a) origin of fold, (b) first plication, (c) second plication, and (d) third plication.

of the first plication. A few specimens with a bicrested fold have been collected. The fold angle becomes increasingly more acute in adulthood, reaching a minimum fold angle that occurs in the range 43 to 47 degrees. This fold angle is significantly less than found in what I consider the main *Enteletes* stock (*E. pugnoides*, *E. churchensis*, and *E. brownvillensis*). NEWELL did recognize the gradational relationship between the imbricated posterior part of *E. plattsmouthensis* and the smooth posterior region of *E. hemiplicatus.*

Internally, *Enteletes hemiplicatus* differs from other species by the presence of an apparently bilobed cardinal process. Other structures differ from those of other species of *Enteletes* only in degree of development. The two lobes apparently develop on either side of a median bladelike structure. When grown beyond the median blade, they are divided by a narrow slit. The bilobed nature of the cardinal process appears to be appreciably different from the smaller trilobed cardinal process of *E. pugnoides* and *E. beilensis* (Fig. 10). The bilobed nature of the cardinal process may be the result of extended growth of the smaller trilobed cardinal process.

Measurements.—Observations on measurements of *Enteletes hemiplicatus* are given as follows.

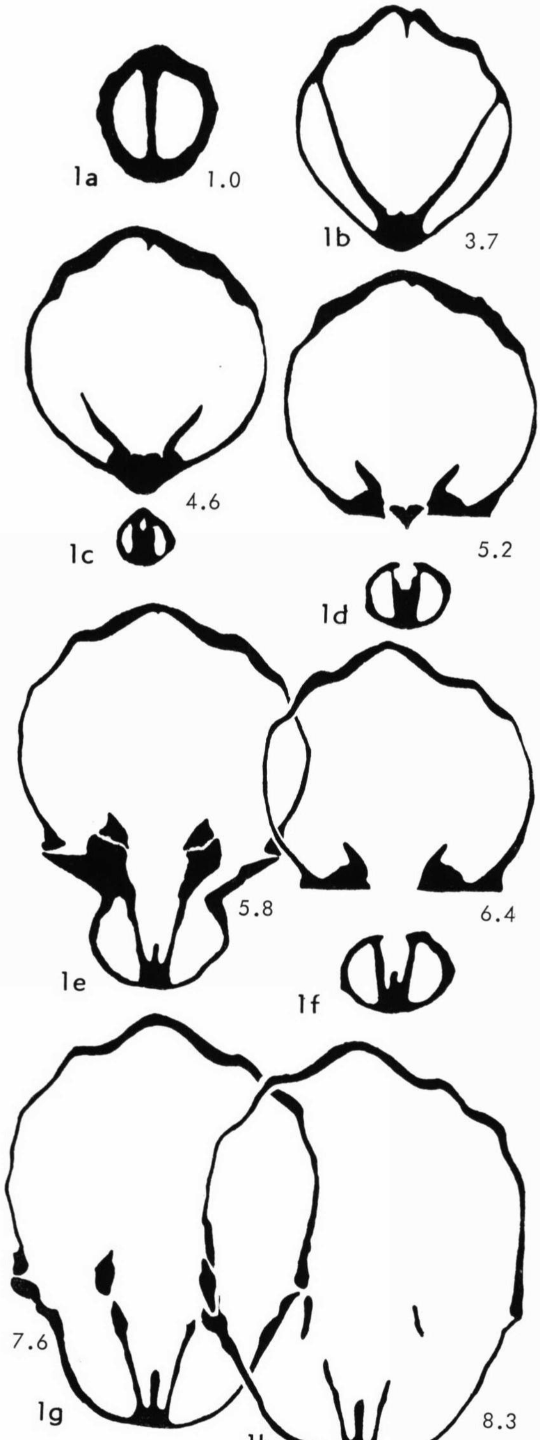

FIG. 10. Serial transverse sections of *Enteletes hemiplicatus* showing distances from pedicle-valve beak in millimeters; specimen from Plattsmouth Limestone in Douglas County, Kansas (sec. 27, T. 14 S., R. 20 E.), ×2.25.

DIMENSIONS

figured specimens	length mm.	thickness mm.	width mm.	fold angle
14006	21.6	23.5	26.2	44°
14007	23.0	22.1	25.2	—
14008	22.1	25.5	26.3	56°

COSTELLAE DENSITY (C/mm.)

distance anterior from dorsal beak	mode	range	N
5 mm.	6.5	6.0 - 7.5	10
10 mm.	6.0	5.4 - 6.3	10

DISTANCES FROM BRACHIAL-VALVE BEAK TO FOLD AND PLICATIONS

	$\bar{x}$	s^2	mode	range	N
fold	9.9	0.4	9.0	7 - 13	35
1st plication	10.8	1.6	11.0	8 - 15	58
2nd plication	12.1	2.4	12.5	9 - 15	57
3rd plication	13.4	2.5	14.0	11 - 17	44

Occurrence.—*Enteletes hemiplicatus*, as described by me, is restricted in occurrence to the Plattsmouth Limestone (Table 4), where it is locally very abundant throughout the entire Plattsmouth outcrop in Kansas. Although *E. pugnoides* and *E. transversus* also occur in the Plattsmouth Limestone, they never occur in association with *E. hemiplicatus*, and are restricted to a slightly different lithology of limestone.

Illustrations.—Plate 3, figure 1; Plate 4, figure 1; Plate 5, figure 1.——Pl. 3, fig. 1a-e, ext. views of specimen (KU 14006) from Plattsmouth Limestone, post., ant., lat., ventral, dorsal, all ×3.——Pl. 4, fig. 1a-d, ext. views of gerontic specimen (KU 14007) from Plattsmouth Limestone, post., ant., lat., dorsal, all ×3.——Pl. 5, fig. 1a-e, ext. views of adult bicrested specimen (KU 14008) from Plattsmouth Limestone, post., ant., lat., ventral, dorsal, all ×3.

ENTELETES BEILENSIS Haglund, new species

Enteletes hemiplicatus (Hall), DUNBAR & CONDRA, 1932, Nebraska Geol. Survey, Bull. 5, 2nd ser., p. 60-62, pl. 2, fig. 7, 12; pl. 44, fig. 3-4a.

Diagnosis.—Large, subspherical shell, with strongly dorsibiconvex longitudinal profile, dorsal outline broadly rounded and nearly circular, maximum width slightly posterior of mid-length, maxi-

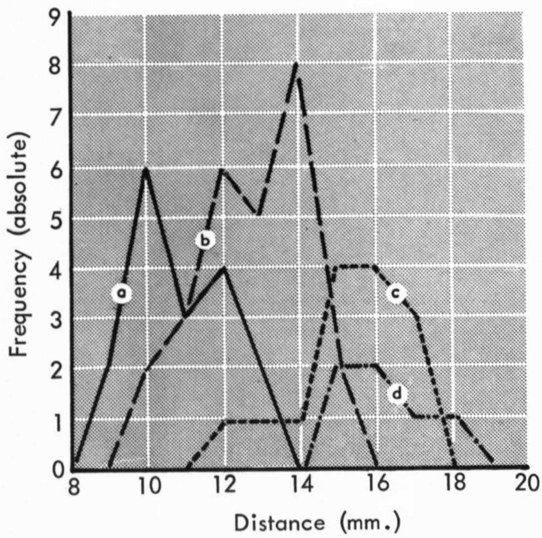

FIG. 11. Graph showing frequency of distances in *Enteletes beilensis* from brachial-valve beak to (a) origin of fold, (b) first plication, (c) second plication, and (d) third plication.

mum thickness slightly anterior of mid-length, maximum length appreciably less than width; dorsal beak moderately broad and pointed, moderately strong incurved; fold unicrested, moderately broad fold angle; 58 to 62 degrees; fold originating at long distance from dorsal beak, a modal distance of 10 mm.; one to three lateral plications beginning at moderately long distance anterior of dorsal beak, first plication a modal distance of 14 mm.; second plication a modal distance of 15.5 mm.; and third plication a modal distance of 15.5 mm.; fine radial ornamentation.

Discussion.—The occurrence of *Enteletes* in the Beil Limestone was first noted by GIRTY (1903, p. 76) and later by DUNBAR & CONDRA (1932, p. 63). The superficial similarity to *E. hemiplicatus* found in the Plattsmouth Limestone caused them to regard the specimens in the Beil Limestone as later occurring specimens of *E. hemiplicatus*. Externally, *E. beilensis* is easily distinguished by its large size, and in this respect is similar to *E. hemiplicatus* (Table 1, 3). The size of the adult is approximately 22 mm. in length; 20 mm. in thickness; and 27.5 mm. in width. The distances from the brachial-valve beak to the origin of the fold and lateral plications, and the fold angle easily distinguish *E. beilensis* from similar Pennsylvanian species of *Enteletes* in Kansas. A comparison of the measurements of *E. beilensis* with other species of *Enteletes* suggests that it is best regarded as a separate species (Tables 1, 2, and Appendix 1).

The fold of *Enteletes beilensis* is unicrested; multicrested forms have not been found. The fold originates as a low, broad vertical deflection at a modal distance of 10 mm. anterior from the brachial-valve beak (Fig. 11), the crest becoming gradually more narrow anteriorly. At the point of geniculation, approximately 23 mm.; the fold continues to possess a moderately broad rounded fold crest with the flanks of the fold small in relation to the thickness of the shell. The fold angle of *E. beilensis* in the adult ranges from 58 to 62 degrees; this is appreciably broader than any other species of comparable size or growth stage.

The lateral plications of *Enteletes beilensis* originate at a relatively long distance anteriorly from the dorsal beak and appear to be very subtle (Fig. 11). The crest of the plications is broad and rounded as in the fold, and develops anteriorly into low broad plications.

As a result of the subtle fold and lateral plications, the longitudinal profile of *Enteletes beilensis* appears extremely circular, the brachial valve showing the strongest convexity; the dorsal outline is also extremely well rounded.

Internally, the basic elements of the genus are present, the most characteristic being the trilobed cardinal process. In viewing a set of serial sections from a specimen of *Enteletes beilensis* the cardinal process was found to be very similar to that found in *E. pugnoides* (Fig. 12).

Measurements.—Data on dimensions of *Enteletes beilensis* follow.

DIMENSIONS

figured specimen	length mm.	thickness mm.	width mm.	fold angle
14009	22.2	20.0	25.2	62°

DISTANCE FROM BRACHIAL-VALVE BEAK TO ORIGIN OF FOLD AND LATERAL PLICATIONS

	$\bar{x}$	s^2	mode	range	N
fold	10.8	3.4	10.0	9 - 13	17
1st plication	12.8	1.2	14.0	10 - 15	26
2nd plication	15.3	1.7	15.5	12 - 17	14
3rd plication	16.2	0.3	15.5	15 - 18	6

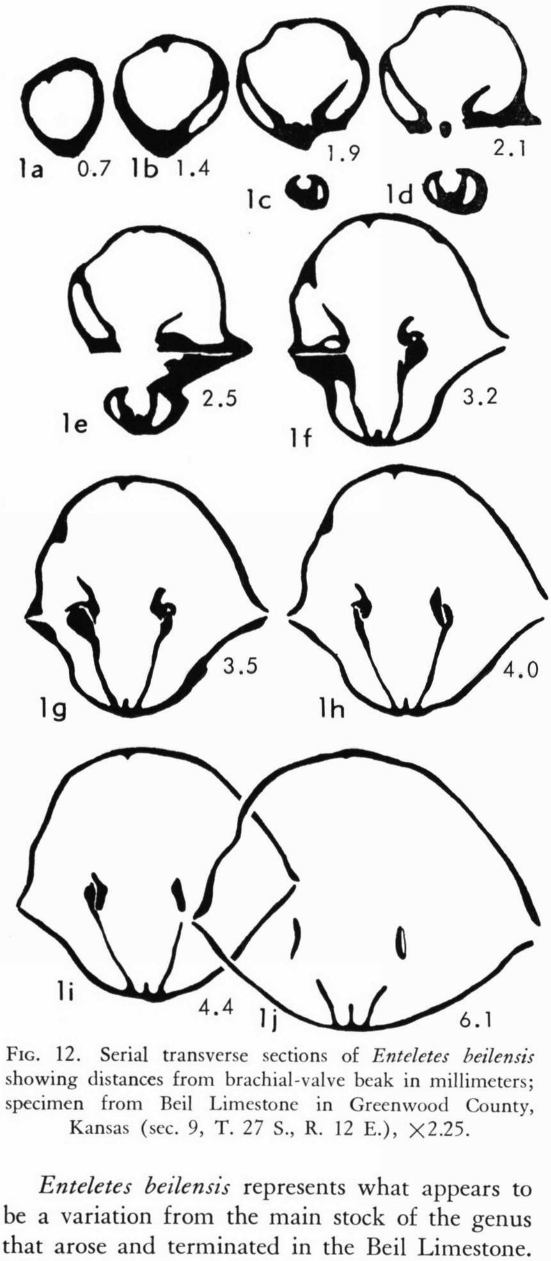

FIG. 12. Serial transverse sections of *Enteletes beilensis* showing distances from brachial-valve beak in millimeters; specimen from Beil Limestone in Greenwood County, Kansas (sec. 9, T. 27 S., R. 12 E.), ×2.25.

Enteletes beilensis represents what appears to be a variation from the main stock of the genus that arose and terminated in the Beil Limestone. The precise relationship of *E. beilensis* to other species of *Enteletes* is uncertain.

Occurrence.—In a comprehensive stratigraphic study of the Beil Limestone in Kansas, BROWN (1958, p. 158, 160) recorded the occurrence of *Enteletes* in only two areas in Kansas, the Marais des Cygnes River area and the Verdigris River area. Collections made by me verify the restricted stratigraphic and geographic occurrence of the species respectively to the Beil Limestone at the two localities noted by BROWN.

Illustrations.—Plate 6, figures 1a-e, ext. views of specimen (KU 14009) from Beil Limestone, post., ant., lat., ventral, dorsal, all ×3.

ENTELETES CHURCHENSIS Haglund, new species

Enteletes hemiplicatus (Hall), DUNBAR & CONDRA, 1932, Nebraska Geol. Survey, Bull. 5, ser. 2, p. 60-63, pl. 2, fig. 7, 12; pl. 44, fig. 3-4a.

Diagnosis.—Medium-sized, subspherical, with strongly dorsibiconvex, moderately narrow, rounded, triangular dorsal outline, maximum width and thickness slightly anterior of mid-length, maximum length slightly more than width; brachial-valve beak moderately narrow and pointed, strongly incurved; with fold usually unicrested, rarely bicrested, unicrested fold moderately acute, minimum fold angle, 48 to 52 degrees, fold originating at moderate distance from beak with modal distance of 9 mm.; one to three lateral plications beginning at moderate distance in front of dorsal beak, first one with modal distance of 9 mm., second with modal distance of 9 mm., and third with modal distance of 10 mm. from beak; fine radial ornamentation.

Discussion.—The occurrence of *Enteletes* in the Howard Limestone was first recorded by GIRTY (1903, p. 26). The specimens collected were believed to be *E. hemiplicatus* (HALL). Specimens from the Howard collected by DUNBAR & CONDRA (1932, p. 64) were assigned by them to *E. hemiplicatus*, which was still regarded as the major species of the genus in the Pennsylvanian of Kansas. Collections made by me indicate that the occurrence of *Enteletes* in the Howard Limestone represents a distinct species (Tables 1, 2 and Appendix 1). The degree of development of the fold and plications from the brachial-valve beak and the adult size of the specimens distinguish it from other species of the genus. Although *E. churchensis* is distinct, it closely resembles *E. pugnoides* in general characters and probably represents a successive stage in the evolution of *Enteletes*. This is exemplified in the point of origin of the fold and lateral plications from the brachial-valve beak (Fig. 13) and the moderate increase in size. The development of the fold ranges from 7.6 to 10.5 mm. from the beak; the mean and mode both occur at a distance of 9 mm. This distance is appreciably greater than in *E. pugnoides*

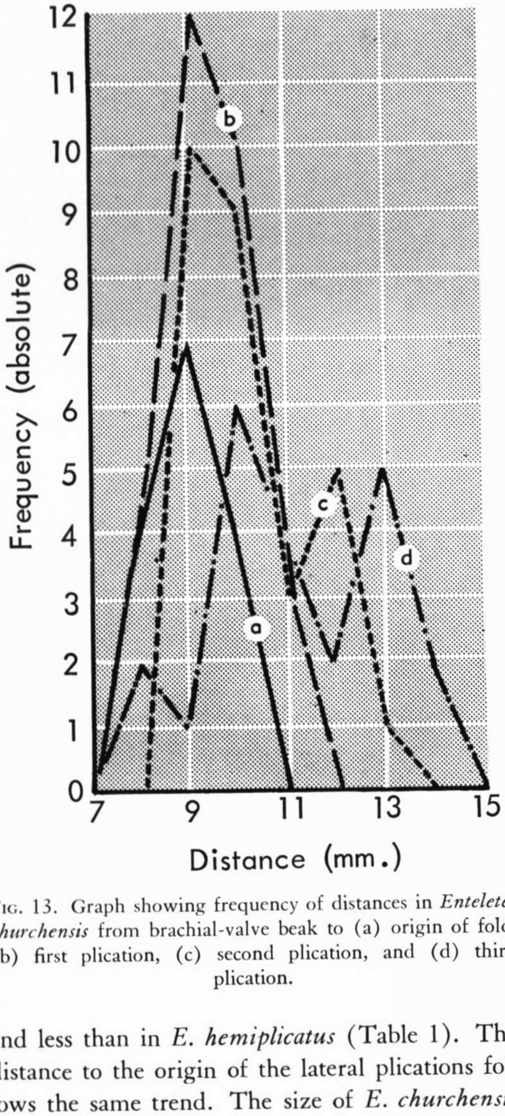

FIG. 13. Graph showing frequency of distances in *Enteletes churchensis* from brachial-valve beak to (a) origin of fold, (b) first plication, (c) second plication, and (d) third plication.

and less than in *E. hemiplicatus* (Table 1). The distance to the origin of the lateral plications follows the same trend. The size of *E. churchensis* is medium, since adult specimens approaching 20 mm. in length and thickness are common; geniculation of the shell appears to begin at a length of approximately 17 mm.

In outline *Enteletes churchensis* is distinctively triangular. From a narrow brachial-valve beak, the sides extend diagonally forward with straight sides rounding into a nearly vertical anterior margin.

The fold of *Enteletes churchensis* is usually unicrested and moderately acute. A single specimen was collected which possessed a distinct bicrested fold.

Measurements.—Observations on the size and some morphological features of *Enteletes churchensis* follow.

DIMENSIONS

figured specimens	length mm.	thickness mm.	width mm.	fold angle
14010	16.9	14.0	19.8	60°
14011	20.8	20.5	22.1	....

DISTANCES FROM BRACHIAL-VALVE BEAK TO FOLD AND LATERAL PLICATIONS

	x	s^2	mode	range	N
fold	9.0	0.5	9.0	8 - 10	15
1st plication	9.4	0.2	9.0	8 - 11	30
2nd plication	10.2	1.8	9.0	9 - 13	28
3rd plication	11.2	2.8	10.0	8 - 14	22

Occurrence.—Moderately well-preserved specimens of *Enteletes churchensis* are locally abundant in the Church Limestone Member. Small samples have been collected from adjacent units to establish the precise stratigraphic range of the species. The oldest collected specimens of *E. churchensis* are from the Howard Limestone and the youngest are from the Bern Limestone (Table 4). More collections may extend the range of the species.

Enteletes churchensis has been found only in Osage and Shawnee Counties in Kansas and appears to be absent in southern Kansas. In Oklahoma, specimens of *Enteletes* sp. are very common in the Church Limestone (MOORE, 1935, p. 208).

Illustrations.—Plate 7, figures 1-2.——Pl. 7, fig. 1a-e, ext. views of specimen (KU 14010) from Church Limestone, post., ant., lat., ventral, dorsal, all ×3.——Pl. 7, fig. 2a-e, ext. views of bicrested specimen (KU 14011) from Church Limestone, post., ant., lat., ventral, dorsal, all ×3.

ENTELETES BROWNVILLENSIS Haglund, new species

Enteletes hemiplicatus (Hall), MUDGE & YOCHELSON, 1962, U.S. Geol. Survey Prof., Paper 323, p. 85, pl. 15, fig. 4, 5.

Diagnosis.—Medium-sized to moderately large, spherical, strongly dorsibiconvex, very broadly rounded, triangular dorsal outline, maximum width and thickness slightly in front of midlength, maximum length less than width; brachial-valve beak moderately broad and rounded, rather strongly incurved; unicrested fold moderately

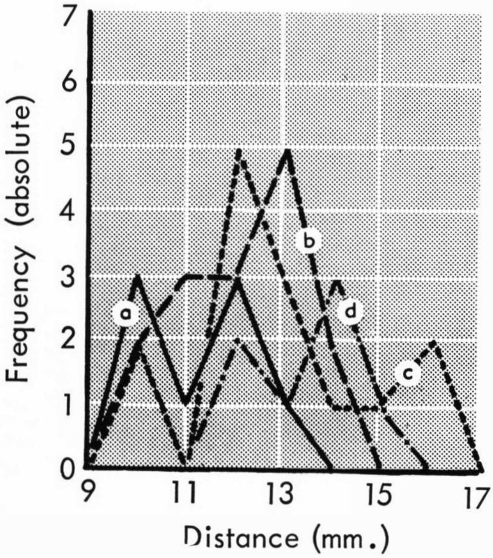

FIG. 14. Graph showing frequency of distances in *Enteletes brownvillensis* from brachial-valve beak to (a) origin of fold, (b) first plication, (c) second plication, and (d) third plication.

broad, minimum adult fold angle 48 to 52 degrees, fold originating at appreciably long distance from beak, with modal distance of 11 mm.; one to three lateral plications beginning an appreciable distance in front of beak (Fig. 14), first plication with modal distance of 12 mm., second with modal distance 13 mm., and third with modal distance of 14 mm.; fine radial ornamentation.

Discussion.—Several specimens of *Enteletes* had been collected by earlier workers (DUNBAR & CONDRA, 1932; MUDGE & YOCHELSON, 1962) from the Wood Siding Limestone and were considered to represent *E. hemiplicatus*. A comparison of specific measurement of specimens of *Enteletes* collected by me with other species of *Enteletes* in Kansas indicate that the specimens differ sufficiently to merit separate designation (Tables 1, 2).

The distance from the beak to the origin of the fold of the Pennsylvanian species of *Enteletes* in Kansas reaches its maximum in *E. brownvillensis* (Table 3). It has a modal distance of 11 mm. To a lesser extent *E. brownvillensis* also represents a trend toward increased shell size, for adult specimens approaching 20 mm. in length are common, with geniculation of the shell beginning at a length of approximately 18.5 mm. The length-thickness ratio is slightly greater in *E. brownvillensis* than in *E. churchensis*, and much greater than in *E. pugnoides* (Table 3).

The minimum fold angle of *Enteletes brownvillensis* (48° to 52°) is similar in range to that of *E. churchensis* and *E. pugnoides*, but relative size of the flanks of the fold in *E. brownvillensis* is appreciably greater than in *E. churchensis* and *E. pugnoides*. The flanks of the fold in *E. brownvillensis* are approximately 3 times greater than the flanks of the first plication.

The nature of the interior of *Enteletes brownvillensis* is not known.

Measurements.—Data on measurements of this new species follow.

DIMENSIONS

figured specimen	length mm.	thickness mm.	width mm.	fold angle
14012	18.8	18.0	24.1	72°

DISTANCE FROM BRACHIAL-VALVE BEAK TO ORIGIN OF FOLD AND LATERAL PLICATIONS

	$\bar{x}$	s^2	mode	range	N
fold	11.3	0.4	11.0	10 - 13	8
1st plication	12.1	2.6	12.0	10 - 14	15
2nd plication	12.9	2.4	13.0	10 - 16	14
3rd plication	13.4	2.0	14.0	12 - 15	7

Occurrence.—*Enteletes brownvillensis* is most abundant in the Brownville Limestone Member of the Wood Siding Limestone (Table 5). The precise stratigraphic range is difficult to establish because of the sporadic and sparse occurrence in the adjacent units. I consider the earliest occurrence of *E. brownvillensis* to be in the Tarkio Limestone where only one or two specimens of *Enteletes* have been collected. Successive units have provided similar-sized samples. The upper limit of the species is not known but possibly extends into Permian rocks. In respect to the great abundance of earlier species of *Enteletes* in Kansas, *E. brownvillensis* occurs with only moderate abundance in the Brownville Limestone (Table 5).

Illustrations.—Plate 8, figures 1a-e, ext. views of specimen (KU 14012) from Brownville Limestone, post., ant., lat., ventral, dorsal, all ×3.

SUMMARY

Enteletes pugnoides found in the Iola Limestone (middle Missourian) of Kansas, is the oldest species of the genus now known in North America. *E. pugnoides* is a small and highly variable species. The number and degree of development of crests of the fold are its most variable features; adult size is less variable.

In the upper Plattsburg and lower Stanton limestones, *Enteletes pugnoides* reaches its greatest abundance, geographic distribution, and variability of the fold. During the remainder of the Missourian Stage *E. pugnoides* rapidly declined in abundance, becoming locally absent at the end of the Missourian (Table 5).

Enteletes pugnoides reappears in the Oread Limestone (early Virgilian) in moderately great abundance, wide geographic distribution, and high variability. During this second occurrence the nature of the fold of *E. pugnoides* is less variable, but shell size and the fold angle are highly variable. In the mid-Oread Plattsmouth Limestone, two new species of *Enteletes (E. transversus, E. hemiplicatus)* appear with *E. pugnoides*. *E. transversus* differs from *E. pugnoides* in increased size of the fold; *E. hemiplicatus* differs from *E. pugnoides* by an appreciable increase in maximum size (Table 1). *E. pugnoides* and *E. hemiplicatus* disappear at the top of the Plattsmouth Limestone. *E. transversus* is last recorded from the lower Lecompton Limestone (Table 4).

In the remainder of the Virgilian the genus appears to become more restricted in occurrence and abundance. This is exemplified by the local occurrence and slight abundance of *Enteletes beilensis* in the Lecompton Limestone. *E. beilensis* is a very large species that is significantly different from any other species. *Enteletes* occurs very sporadically elsewhere in the Virgilian. In the Howard Limestone, the genus appears in increased abundance, being represented here by *E. churchensis*. This species appears to have been derived from *E. pugnoides*, possibly representing a stage in its evolution.

By the end of Pennsylvanian time, *Enteletes* had become moderately uniform in character and abundance. The genus is represented by *E. brownvillensis*, a species that appears to be a continuation of the *E. pugnoides-E. churchensis* series. That *E. pugnoides* and *E. churchensis* represent successive stages in the main stock of *Enteletes* is suggested by the uniform increase in 1) size and 2) distance from the brachial-valve beak to the origin of the fold. The fold angle is moderately uniform for the three species.

Enteletes transversus, *E. hemiplicatus* and *E. beilensis* are considered by me to represent unsuccessful offshoots of *Enteletes* that quickly become extinct.

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APPENDIX

Student t-test of mean distance from dorsal beak to origin of the fold for similar species of *Enteletes*.

$$t = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{1/N_1 + 1/N_2}} \qquad \sigma = \sqrt{\frac{N_1 s^2_1 + N_2 s^2_2}{N_1 + N_2 - 2}}$$

1. *Enteletes pugnoides* and *Enteletes hemiplicatus*
$\bar{x}_1 =$ *E. pugnoides*
$\bar{x}_2 =$ *E. hemiplicatus*
0.05 level of significance
$\bar{x}_1 \leqq \bar{x}_2$

$$\sigma = \sqrt{\frac{(143)\ (1.0) + (35)\ (0.4)}{(143) + (35) - 2}} = 0.973$$

$$t = \frac{(6.4) - (9.9)}{0.973 \sqrt{1/143 + 1/35}} = -1.90$$

Therefore $\bar{x}_1$ is significantly less than $\bar{x}_2$

2. *Enteletes pugnoides* and *Enteletes churchensis*
$\bar{x}_1 =$ *E. pugnoides*
$\bar{x}_2 =$ *E. churchensis*
0.05 level of significance
$\bar{x}_1 \leqq \bar{x}_2$

$$\sigma = \sqrt{\frac{(143)\ (1.0) + (15)\ (0.5)}{(143) + (15) - 2}} = 0.982$$

$$t = \frac{(6.4) - (9.0)}{0.982 \sqrt{1/143 + 1/15}} = -9.80$$

Therefore $\bar{x}_1$ is significantly less than $\bar{x}_2$

3. *Enteletes churchensis* and *Enteletes brownvillensis*
$\bar{x}_1 =$ *E. churchensis*
$\bar{x}_2 =$ *E. brownvillensis*
0.05 level of significance
$\bar{x}_1 \leqq \bar{x}_2$

$$\sigma = \sqrt{\frac{(15)\ (0.5) + (8)\ (0.4)}{(15) + (8) - 2}} = 0.714$$

$$t = \frac{(9.0) - (11.3)}{0.714 \sqrt{1/35 + 1/8}} = -21.00$$

Therefore $\bar{x}_1$ is significantly less than $\bar{x}_2$

4. *Enteletes hemiplicatus* and *Enteletes beilensis*
$\bar{x}_1 =$ *E. hemiplicatus*
$\bar{x}_2 =$ *E. beilensis*
0.05 level of significance
$\bar{x}_1 \leqq \bar{x}_2$

$$\sigma = \sqrt{\frac{(35)\ (0.4) + (17)\ (3.4)}{(35) + (17) - 2}} = 1.20$$

$$t = \frac{(9.9) - (10.8)}{1.20 \sqrt{1/35 + 1/17}} = -2.54$$

Therefore $\bar{x}_1$ is significantly less than $\bar{x}_2$

5. *Enteletes beilensis* and *Enteletes brownvillensis*

$\bar{x}_1$ = *E. hemiplicatus*

$\bar{x}_2$ = *E. brownvillensis*

0.05 level of significance

$\bar{x}_1 \leqq \bar{x}_2$

$$\sigma = \sqrt{\frac{(17)\ (3.4) + (8)\ (0.4)}{(17) + (8) - 2}} = 1.63$$

$$t = \frac{(10.8) - (11.3)}{1.63 \sqrt{1/17 + 1/8}} = -7.15$$

Therefore $\bar{x}_1$ is significantly less than $\bar{x}_2$